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THE DEVELOPMENT OF THE SPHENOIDAL SINUS IN MAN AND ITS HOMOLOGY IN MAMMALS

By P. H. G. van GILSE, M.D. (Amsterdam)

The hinder part of the nasal cavity in the Mammals, with the exception of the Primates, is provided, as has been observed by Dursy, with a double floor. Of this double floor, the lower stage is the palate, the upper the laminae

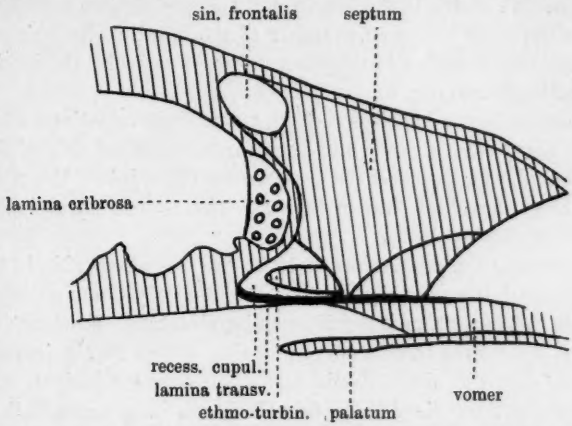

Fig. 1. Skull of adult dog. Sagittal section. Schematic. Posterior-inferior part of septum resected to show the inferior turbinal.

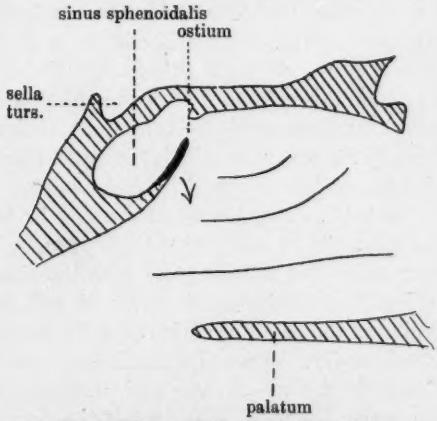

Fig. 2. Human skull. Sagittal section.

transversales and between the two is the ductus naso-pharyngeus which is continuous with the lower part (pars respiratoria) of the nasal cavity.

Dursy states that a similar division of the hinder part of the nasal cavity into olfactory and respiratory parts would be present in man if the conchae Bertini, which form the front wall of the sphenoidal sinus, were turned downwards, as in his opinion the conchae Bertini correspond to the laminae transversales. He compares them to a drawbridge which is pulled up in man and lowered in most other Mammals (fig. 2).

Before Dursy the homology of the conchae Bertini and the laminae transversales had already been formulated by Cleland. Dursy pursued the subject further by studying mammalian embryos in which the nasal capsule is still cartilaginous. He states that even in early stages similar conditions are to be seen: an upper or olfactory chamber of the nasal cavity being separated from a respiratory chamber or ductus naso-pharyngeus by the laminae transversales (cartilagineae) (fig. 3).

In human embryos he observed very small prolongations of the upper part of the nasal cavity extending backwards on either side of the cartilaginous sphenoid. These small recesses are, in his opinion, the rudiments or *Anlage* of the sphenoidal sinuses (fig. 4). The cavum naso-pharyngeum is situated below these recesses.

Dursy came to the conclusion that the recesses observable in the human embryo represent the posterior part of the olfactory chamber of Mammals. He says: "Somit besitzt auch der Mensch im hintersten Abschnitt der Nasenhöhle eine Abscheidung in eine obere und eine untere Partie, jedoch mit dem Unterschied, dass die obere Partie nur einen äusserst kleinen Anhang der Regio olfactoria oder die Anlage der Keilbeinhöhlen darstellt." These recesses grow into the sphenoid, where they give rise to the permanent sphenoidal sinuses. Later authors (Toldt, Zuckerkandl, etc.) confirm Dursy's opinion.

It seems to me, however, that the problem needs further investigation, for: (1) The comparison of the conchae Bertini to a drawbridge, which is pulled up in man, is open to criticism. Primitively, the conchae Bertini are not concerned in providing the front wall of the sphenoidal cavity only, as Bertini himself described them as *plates* bent upon themselves. Toldt has taught us that originally the concha Bertini is the ossified cartilaginous capsula posterior nasi which is completely closed behind. A bony capsule, which is closed on all sides with the exception of an opening in front and which is separated from the sphenoid by connective tissue, can be isolated in young children. At a later stage this capsule fuses with the sphenoid. After this fusion has taken place the posterior wall is absorbed, and the pneumatisation of the sphenoid begins as the result of an invasion by the mucous membrane which lines the nasal cavity. These changes I have described and briefly discussed in the *Zeitschrift f. Hals-, Nasen- und Ohren-heilkunde.* Thus of the original bony capsule the front wall and part of the floor alone persist and they also form the front wall and part of the floor of the sphenoidal sinus. These persisting parts of the nasal capsule are the "conchae sphenoidales" of Bertin. (2) Dursy states in his article (p. 197): "Auch bei den Säugetieren

greift das hintere Ende der Regio olfactoria in die Keilbeingegend ein, aber in viel stärkerem Masse, sodass aus diesem Grunde besondere Keilbeinhöhlen nicht verkommen, oder es bilden vielmehr diese Höhlen bei den Säugern

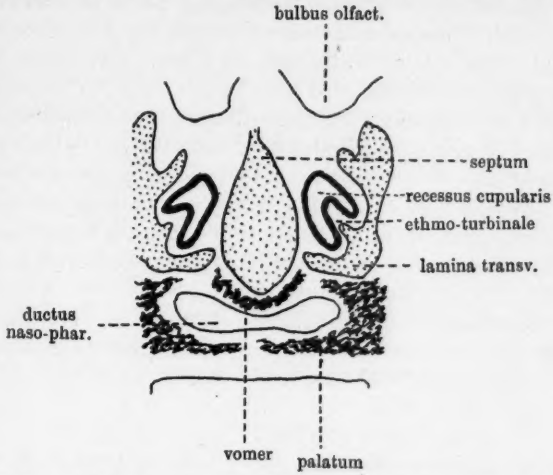

Fig. 3. Embryo of *Ovis aries*. Frontal section through the posterior part of the nose.

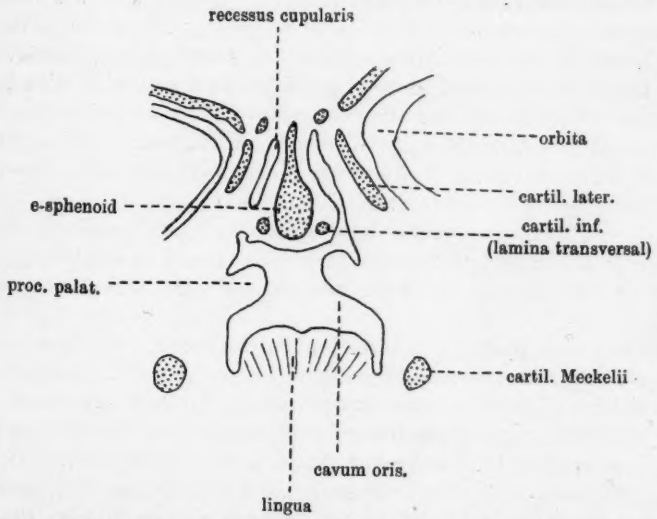

Fig. 4. Human embryo of 26 mm. length. Frontal section through the posterior part of the nose.

keinen Anhang der Nasenhöhlen, sondern gehen gänzlich in die Nasenhöhlen auf." According to this view the part of the nasal cavity which lies above the laminae transversales is represented by the widened sphenoidal sinus

(p. 96). He particularly emphasises the fact that he never found a true sphenoidal sinus in adult Mammals. The view that a sphenoidal sinus is non-existent in Mammals is, however, a misconception. Certainly there are Mammals which have no sphenoidal sinuses, e.g. *Canis familiaris*, but there are others in which a true sphenoidal cavity exists, e.g. *Felis domestica*, where the sphenoidal cavity communicates with the general nasal cavity by a somewhat narrow entrance.

If there is a strict homology between the laminae transversales and the conchae Bertini, it should be possible to demonstrate: (1) that the osseous laminae transversales of the adult animal are simply parts of a bony capsule limiting the posterior part of the nasal cavity; (2) that the real sinus within the sphenoid, as occurs in the adult cat, is the result of a pneumatisation of the sphenoid by the mucous membrane lining the posterior part of the nasal cavity.

In order to determine these points I studied the development of the posterior part of the human nasal cavity and compared it with that in several Mammals, more especially with that in the cat.

HOMO

If a sagittal section of the nose of a human embryo of 50 mm. length (fig. 5) be examined, the posterior part of the cartilaginous nasal capsule (cupula nasi posterior) is seen to be entirely separated from the basal plate (the cartilaginous precursor of the bony sphenoid). The recess of the nasal cavity lodged in the cupula is the rudiment or *Anlage* of the sphenoidal sinus. Below the recess is a small piece of cartilage. In a coronal section through the posterior part of the nose of a younger human embryo of 25 mm. (fig. 4) the same piece of cartilage again appears below the recess. This cartilage is the remnant of the lamina transversalis, which in animals forms a continuous floor for the regio olfactoria (fig. 3).

As a result of examining a large number of serial sections of human embryos, I found that there were three chief stages in the developmental history of the posterior end of the nasal capsule surrounding the sphenoidal sinus.

The *first stage* was seen in three human embryos (of 34, 55 and 56 mm. length). The cartilaginous skeleton is here composed of a median part, which develops later on into the bony presphenoid, and two lateral parts, one on either side. There is a slight fusion between these medial and lateral parts in the upper part of the nasal cavity (fig. 6, embryo of 56 mm.).

In the *second stage*, which was found in four embryos of 36, 59, 70 and 90 mm. respectively, not only has the upper connection between the medial and lateral cartilages become more extensive, but a second and lower connection has made its appearance between them. Further, in coronal sections of the anterior part of the sinus capularis a downwardly growing process of the medial cartilage is apparent. If serial sections of these embryos are traced

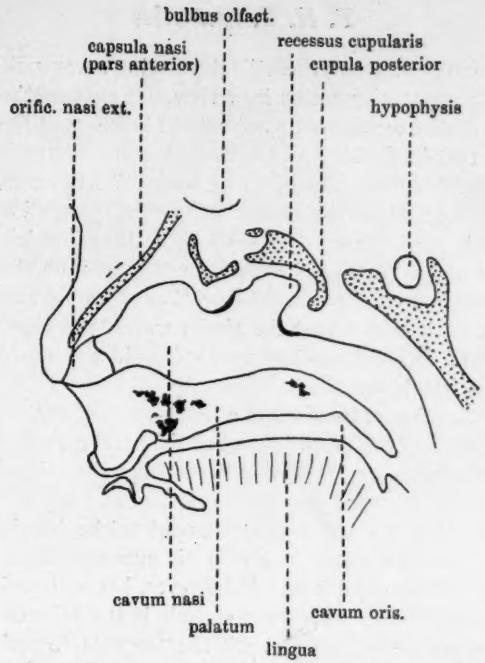

Fig. 5. Human embryo of 50 mm. length. Sagittal section of the nose.

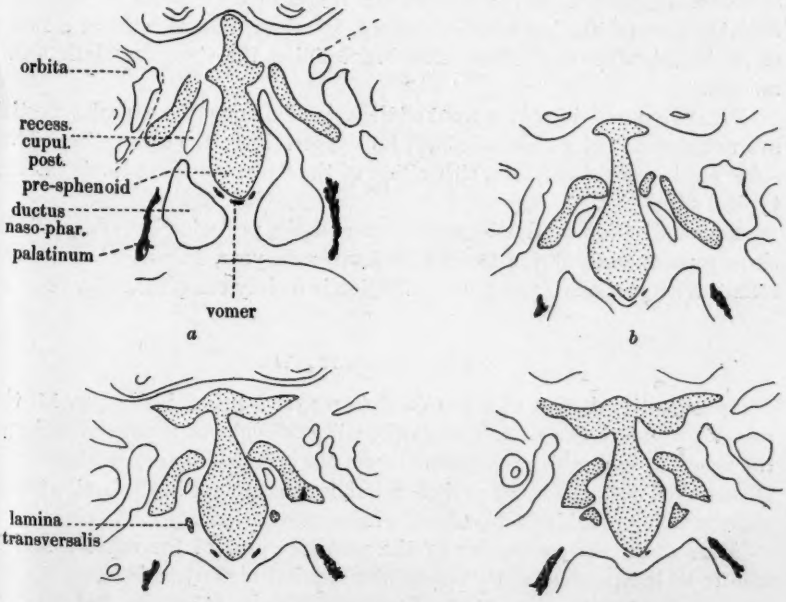

Fig. 6 (*a–d*). Human embryo of 56 mm. length. Frontal sections: *a*, through the entrance of the *recessus cupularis*; *d*, behind the *recessus*.

from before backwards, a closed cartilaginous ring surrounding the recess of the nasal cavity eventually comes into view. The connections between the lateral and the medial cartilages do not extend throughout the capsule. Thus it comes about that in the hindmost sections the medial and lateral cartilages are entirely separated from each other by connective tissue (fig. 7).

In the *third stage*, which was found in three embryos, all 90 mm. long, the sinus cupularis is surrounded on all sides by cartilage, which in this stage is more extensive and is disposed in the form of a tube unconnected with the median cartilage (fig. 8). In a sagittal section of an *older human embryo* of 4½ months (fig. 9), it is seen that the hinder wall of the cupula posterior and the front part of the still cartilaginous sphenoid are separated from each other by connective tissue.

In a sagittal section of the head of a *new-born child* (fig. 10), it can be seen that the ossification of the posterior end of the nasal capsule has commenced, but it is still separared by connective tissue from the sphenoid which is now ossified.

When ossification, the details of which need not be described here, is completed, the recessus cupularis (posterior) is surrounded on all sides, even posteriorly, by a bony capsule which, however, has an opening or deficiency in its front wall (fig. 11). This bony capsule is the fully developed concha, or perhaps it would be better to term it the "capsula," Bertini.

The connective tissue between the osseous cupula nasi posterior and the sphenoid disappears. It is not until the fusion of these parts is completed that the pneumatisation of the sphenoid, by absorption of bone as a result of its invasion by the mucous membrane lining the sinus cupularis, commences.

Fig. 12 is a drawing of the front of the sphenoid bone (the capsulae Bertini are not present) of a child of about four years. Here the absorption of the sphenoid has commenced on either side at the "planum resorptionis" in the typical situations.

Pneumatisation gradually progresses and the posterior boundary of the sinus recedes until at the twelfth or fourteenth year, in normal cases, the sella turcica is reached and penumatisation is mainly completed (fig. 13).

FELIS DOMESTICA

In a sagittal section of a foetal cat (some days before birth) (fig. 14) the recessus cupularis is seen to occupy the still cartilaginous cupula posterior of the nasal capsule, which is separated from the sphenoid by connective tissue. Ossification, both endo- and peri-chondral, is commencing in the lamina transversalis which provides a floor for the recessus cupularis.

Here again the ossification of the posterior part of the capsula nasi is seen to be independent of the sphenoid which has already ossified.

A similar section of a kitten a few weeks old (fig. 15) shows that the pre-

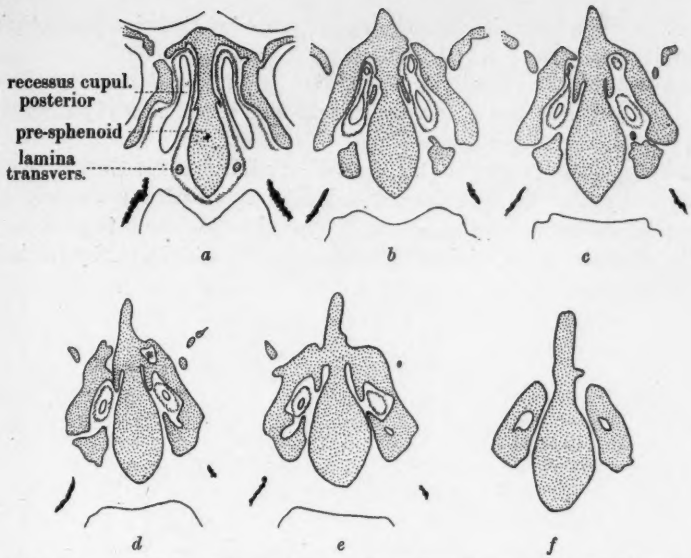

Fig. 7 (*a–f*). Human embryo of 70 mm. length. Frontal sections: *a*, through the entrance of the *recessus cupularis*; *f*, behind the *recessus*.

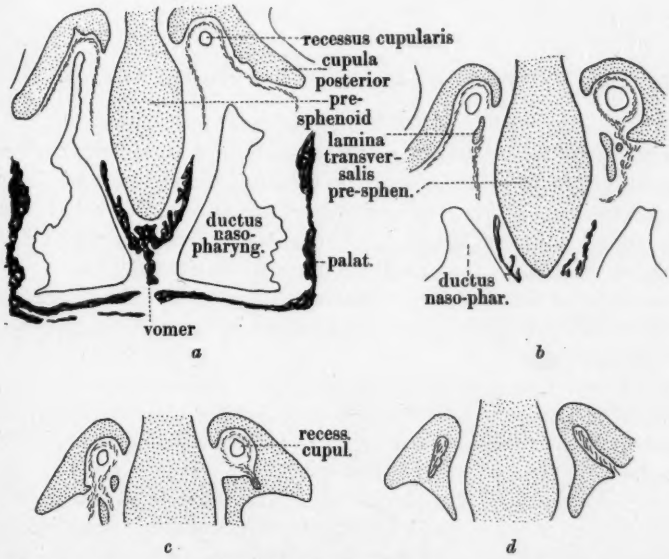

Fig. 8 (*a–d*). Human embryo of 90 mm. length. Frontal sections: *a*, through the entrance of the *recessus cupularis*; *d*, behind the *recessus*.

sphenoid is still unoccupied by a sinus; the (posterior-) inferior ethmo-turbinal now projects into the recessus cupularis.

In a young cat with milk teeth (fig. 16) pneumatisation of the sphenoid has commenced and a cavity extends backwards about half-way through the pre-sphenoid.

In a paramedian section of the skull of an adult cat (fig. 17) a large cavity is seen occupying the pre-sphenoid and extending backwards nearly as far as the post-sphenoid, in other words, a true sphenoidal sinus is present.

The situation of the original recessus cupularis is indicated by the inferior ethmo-turbinal.

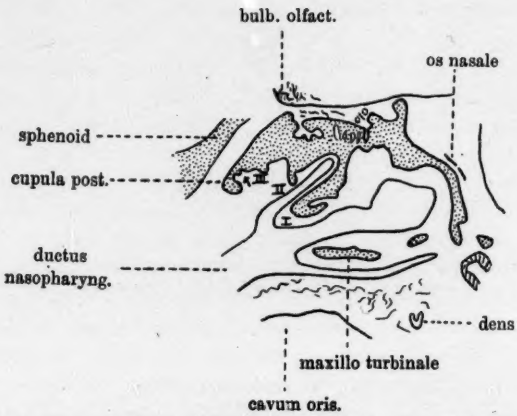

Fig. 9. Human embryo of 4½ months. Sagittal section of the nose.

CANIS FAMILIARIS

As has already been noted, a coronal section of an embryo of 60 mm. in the region of the posterior end of the cartilaginons cupula nasi shows that the regio olfactoria of the nasal cavity is separated from the regio respiratoria by the lamina transversalis (fig. 3). The postero-inferior concha projects into the sinus cupularis, the lining wall of which is invaginated.

If sections of the structures situated further backwards are examined it is seen that the cartilage of the cupula posterior is separated from the sphenoid by connective tissue.

The examination of a sagittal section of the skull of an adult dog (fig. 1) shows that a recessus cupularis exists and that the ossified cupula posterior is fused with the sphenoid, but as no pneumatisation of the sphenoid has taken place, no true sphenoidal sinus exists.

Thus the conditions of affairs in the adult dog correspond in general with those in the cat of a few weeks old: the recessus cupularis posterior exists in both, but in neither is there a pneumatic cavity within the sphenoid.

In the cat, however, as in man, the recessus extends backwards by a secondary pneumatisation of the sphenoid, after the ossified cupula posterior

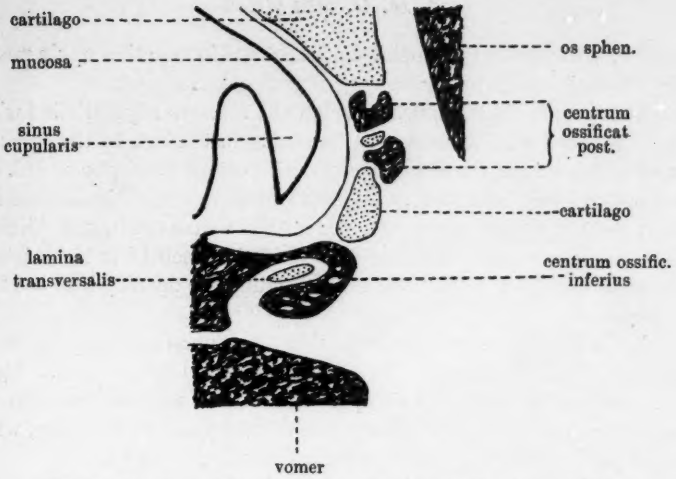

Fig. 10. New-born child. Sagittal section through the *sinus cupularis*.

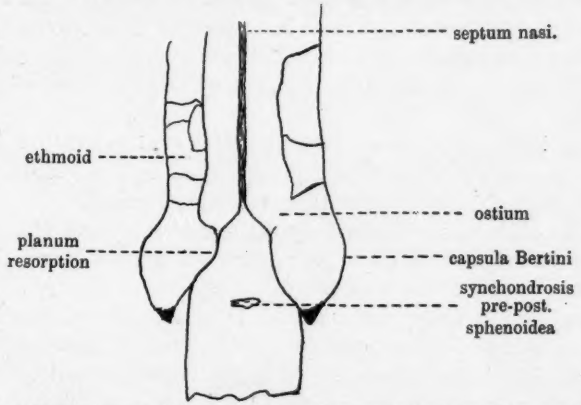

Fig. 11. Child of about 6 years. Schematic horizontal section through the sphenoid and posterior part of the ethmoid. Beginning of (secondary) pneumatisation.

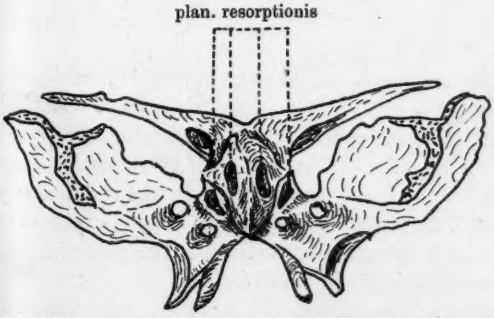

Fig. 12. Frontal aspect of the sphenoid of a child of about 4 years.

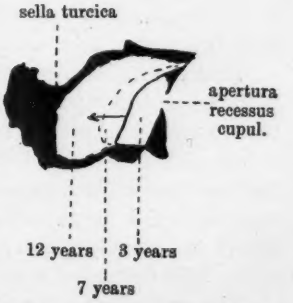

Fig. 13. Schematical sagittal section of the human sphenoid with indication of different stages of development of the sinus.

has fused with the ossified sphenoid. In the cat and in man the cupula posterior and the sphenoid ossify independently of each other.

The human sphenoidal sinus, in which the recessus cupularis is included, is to be compared with the conditions existing in the cat, to the sphenoidal cavity of which animal the recessus cupularis posterior must be added.

Zuckerkandl said that in animals with five and more "Riechwülste in der medialen Reihe" a part of the fifth (or more) is situated in the "Keilbeinnische." In man a remnant of such a "Keilbeinmuschel" is to be found as the supero-lateral part of the front wall bounding the opening into the "sinus sphenoidalis."

In fig. 9, which represents the conditions in a human embryo of 4½ months, the position of this rudimentary turbinal is indicated by an arrow. The rest of the front wall is formed by an upgrowing fold of mucous membrane containing connective tissue (fig. 10) in which dermal ossification occurs, whereas the upper part ossifies by endochondral ossification.

Occasionally a fine fissure is found in the front wall of the sphenoidal sinus in adult human skulls and when present indicates the line of junction of the two parts of which this wall is composed. The curved spiral edge bounding the opening into the sinus which was found in the specimen represented by fig. 18, may be explained as an exhibition of a characteristic feature of a turbinal.

An irregularity, which may have the form of a process, of the lateral cartilaginous wall of the recessus cupularis found in some human embryos (fig. 7) can be considered as a remnant of another turbinal.

The body of the sphenoid normally consists of two parts, viz. the ossified anterior part of the basal plate (post- with pre-sphenoid) and the ossified cupula posterior of the nasal capsule.

The front wall of the sphenoidal sinus together with the anterior part of the sinus in man and the anterior part of the sinus in those animals which possess a true sphenoidal sinus belong to the cupula posterior of the nasal capsule (recessus cupularis posterior). In animals in which a pneumatised sphenoid does not exist, the front wall of the pre-sphenoid together with a recessus behind the inferior ethmo-turbinal ("Keilbeinnische") also belong to the cupula. The lamina transversalis, or its rudimentary representative in man, is a part of this cupula.

That the rudiment (*Anlage*) of the sphenoidal sinus of man is homologous with the posterior part of the regio olfactoria may be taken as proved, but that in man as compared with other animals a relative "withdrawal" ("sich Zuruckziehen") of the ethmoid or of the turbinals from the sphenoidal sinus has taken place (Zuckerkandl) is not a legitimate conclusion. The rudimentary turbinal, which forms part of the front wall of the sinus in man, occupies very nearly the same position in the recessus cupularis as does the posterior end of the fully developed concha sphenoidalis in the cat.

Zuckerkandl's statement that: "den Höhlen des Keilbeins fällt demnach

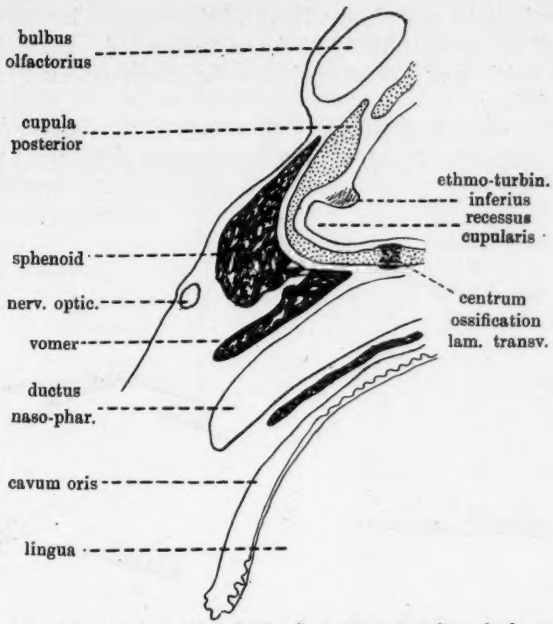

Fig. 14. *Felis domestica* some days before birth. Sagittal section through the posterior part of the nose. Ossification of the lamina transversalis in beginning.

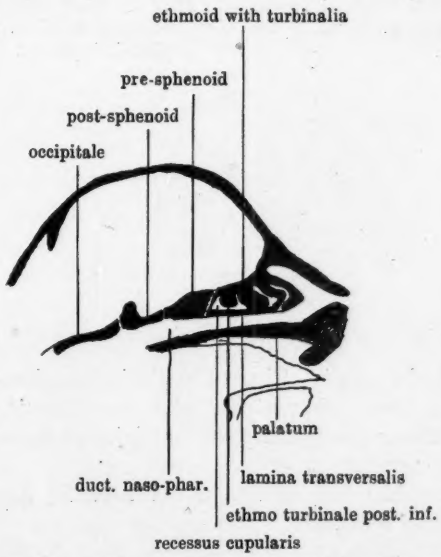

Fig. 15. *Felis domestica* a few weeks old. Sagittal section of the skull.

vielfach die Aufgabe zu, Riechwülste zu beherbergen" is inexact. Paulli's opinion that the sinus sphenoidalis is an "abgeschnittener Teil der Regio olfactoria," which in appearance only has the characteristics of a pneumatic cavity, is a fallacy.

The cavity, which is bounded by the cupula nasi posterior cartilaginea or ossea (concha) Bertini, I propose, at the suggestion of Professor Bolk, to call

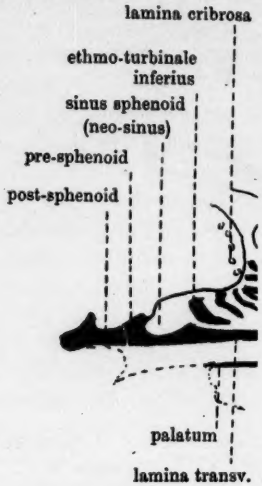

Fig. 16. *Felis domestica* with milk-teeth. Beginning of pneumatisation of the sphenoid.

Fig. 17. Adult *Felis domestica*. Sagittal section of the skull. A sinus within the sphenoid is present.

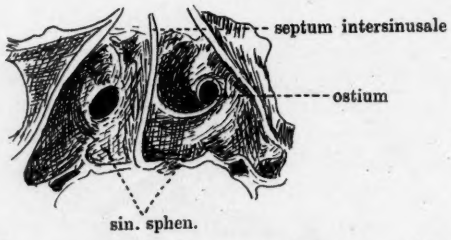

Fig. 18. Inner aspect of the sphenoidal sinus of an adult man.

the palaio-sinus (sphenoidalis). The cavity within the sphenoid, which appears after the fusion of the cupula posterior with the sphenoid and results from the absorption of bone due to the growth activity of the mucous membrane, may be called the neo-sinus.

Thus the sphenoidal sinus of man, as it is normally described, consists of a palaio-sinus plus a neo-sinus.

The palaio-sinus is present in those animals which have no cavity in the sphenoid and is represented in them by the recessus cupularis posterior.

In animals with a pneumatised sphenoid, e.g. the cat, the part of the "sphenoidal sinus" which contains the posterior end of the inferior ("sphenoidal") turbinal is palaio-sinus, the rest of the cavity being neo-sinus.

Finally I wish to emphasise the fact that the epithelium which lines the cavity of the recessus cupularis in the human embryo (fig. 19 *a*) is obviously thinner than in those parts of the nose where olfactory mucous membrane never appears (fig. 19). This thicker epithelium, which is especially obvious in the upper part of the recessus, resembles the epithelium in those parts where, at a later stage, the olfactory mucous membrane makes its appearance.

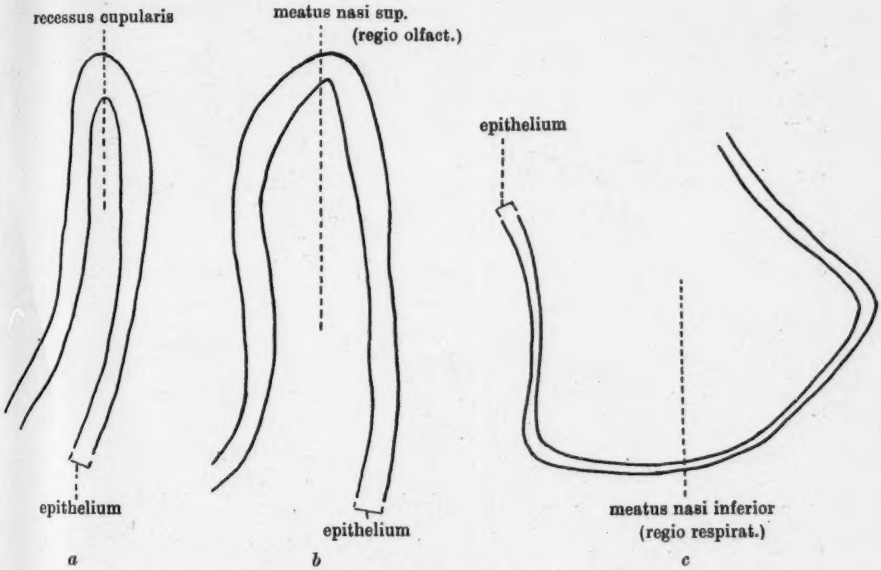

Fig. 19 (*a–c*). Schematic drawings of the thickness of the epithelium in different parts of the human embryonic nose.

That this epithelium is peculiar is very evident under high magnification, as an indication of a membrana limitans can be detected, while here and there nerve fibres of the bulbus olfactorius seem to be connected with the epithelial cells.

This histological evidence supports the view, that the Anlage of the sphenoidal sinus in the human embryo is a part of the olfactory chamber.

All investigators, indeed, are of the opinion that in adults the sphenoidal sinus, including even its anterior part, has no sensory epithelium. The investigations of E. Read, however, show that in the noses of young individuals

the surface of olfactory epithelium is relatively more extensive than it is in adults. Consequently, a diminution of the sensory epithelium of the recessus cupularis in later developmental stages is not a matter for surprise. The epithelium of the mucous membrane of the sinus in a new-born child is also of the same non-olfactory character as that of the accessory sinuses of adults.

SUMMARY

1. The "sphenoidal sinus" of adult man consists of two parts, viz. the recessus cupularis posterior capsulae nasi (palaio-sinus) and the proper cavity in the ossified front part of the basal plate (neo-sinus).

2. The neo-sinus is formed by a secondary pneumatisation of the bone.

3. In animals which have no pneumatised sphenoid the palaio-sinus is represented by the recessus cupularis posterior of the olfactory chamber.

4. In those animals which have a cavity in the sphenoidal bone, this is the result of a secondary pneumatisation and corresponds to the neo-sinus of man.

5. The epithelium of the mucous membrane in the palaio-sinus of the human embryo presents the features of embryonic olfactory epithelium.

6. The opinion of Dursy, viz. that the sphenoidal sinus of man is homologous with the posterior part of the olfactory chamber of quadrupeds, is essentially correct, but his argument supporting this view cannot be accepted.

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THE ARTERIES OF THE BRAIN OF THE ORANG-UTAN

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INTRODUCTION

The arteries of the brain of the Orang-utan have substantially the same distribution and variation as those of the human brain. Apart however from the general interest of the description of the vessels themselves, their method of distribution and variation leads to a clearer understanding of the principles which govern the arrangement and development of arteries generally. The clinical importance of the enunciation of such principles is obvious.

I have to acknowledge that the description of the vessels in the Orang would lack finality if it were not for the work of Stopford (1) on the vessels of the hindbrain in man; for the method of injection used in my specimen was unsuitable for the determination of their internal distribution. Any discussion and presumption, therefore, concerning the internal distribution of the vessels in the Orang are the result of his work in the case of the vessels of the hindbrain, and of the work of Beevor (2) in the case of the forebrain.

The hypothesis which is advanced to explain the principles underlying the distribution of arteries is the outcome of the writings of John Hilton (3), and the result of an association with Professor Elliot Smith who suggested to me the determination of the blood supply of the claustrum. He (4), himself, appreciated the phylogenetic constancy of arteries as a factor in the interpretation of morphological problems when he wrote: "One of the most remarkable items of evidence in corroboration of the reality of homologies expressed in these diagrams is the constancy of the position of relations of the lateral striate artery.... In any mammalian or reptilian brain this arrangement will be found."

The constancy of the position of the anterior spinal artery in any embryo, pointed out by Dart and myself (5), the diagrammatic picture of the hypoglossal nucleus supplied by the same artery, as described by Stopford, and finally the distribution of the internal maxillary artery in the supply of the whole of the masticatory apparatus, including the incudo-malleolar joint—the morphological lower jaw—drew my attention, four years ago, to the hypothesis that arteries are laid down with precision, that they are ontogenetically and phylogenetically stable, and that their constancy is due in all probability to their nerve supply, which is distributed in such a manner as to adopt functional areas.

The hypothesis is applied to all stages in the life of the animal; it is in the embryo that the phylogenetic constancy of the vessels has always proved a

stumbling block to those who would attribute the arrangement of the vessels to mechanical causes. The hypothesis was first stated by me in reference to the artery of the claustrum. The reality of the homologies in this region was confirmed by the vascular distribution. Since then the late John I. Hunter has given remarkable confirmation to those observations in the unravelling of the striatal complex in the forebrain of *Apteryx australis* (6).

The postulates of Thoma were unsatisfying as an adequate explanation of the anatomical facts, and yet, at that time, the multiple functional supply of such an artery as the vertebral appeared to favour, in some measure, a more mechanical explanation. The evidence which can now be advanced explains the development and distribution of these arteries, although difficulties still arise in explaining the multiple blood supply of such a single cell as the motor cell of the Rolandic area and its axon. I am convinced, however, that the hypothesis, that the sympathetic nerve cells arise in common with the arteries as part of a functional mechanism, explains the fact in a more adequate manner than heretofore.

It is generally held that the arteries of the body are not laid down with that precision which marks the distribution of the nerves. Distribution of the vessels is commonly dealt with as though the vessels had little relationship with functional demands. The variations in origin of arteries (not of their final distribution) has been regarded as evidence of this very lack of precision, whereas it will be shown that it is in the variations of arteries that the principles of their distribution are most clearly seen.

The history of this question is both illuminating and interesting. John Hunter (7) put forward the views which are in great part still held to-day. He contrasted the distribution of the nerves with that of the arteries, and came to the conclusion that:

> If their (the nerves) physiology was sufficiently known, we should find the distribution and complication of nerves so immediately connected with their particular uses, as readily to explain many of those peculiarities for which it is now so difficult to account. What naturally leads to this opinion is, the origin and number of nerves being constantly the same, and particular nerves being invariably destined for particular parts, of which the fourth and sixth pair of nerves are remarkable instances. We may therefore reasonably conclude, that to every part is allotted its particular branch, and that however complicated the distribution may be, the complication is always regular.... We observe no such uniformity in vessels carrying fluids,....The course of the arteries is such as will convey the blood most conveniently, and therefore not necessarily uniform....Whoever therefore, discovers a new artery, vein or lymphatic adds little to the stock of physiological knowledge.

His writings on the distribution of vessels are concerned with mechanical, rather than with functional, principles. He observed very closely their methods of branching, of anastomosing and of terminating. He discovered end arteries —a discovery usually attributed to Cohnheim. John Hunter went further than this, however, for he made the one observation which clearly proved that

the origin and primitive distribution of blood vessels has nothing whatever to do with the mechanical forces due to the heart's action.

The vessels are probably the very first active parts in the system, for we find them in action before they have formed themselves into a heart, and in such a state of parts we find them the only part that has any strength, while the other parts are only preparing for action; this is so remarkable, that we can dissect the vessels of a chicken in the egg without injection, the other parts easily giving way (p. 195).

Hunter, therefore, left us three important observations which are not open to dispute: (1) The nerves are constant; (2) Certain vessels are end arteries; and, (3) The vessels are laid down before the heart functions. It is unfortunate that Hunter did not know that the fibres of the sympathetic nervous system are distributed to the walls of the blood vessels, for the method of distribution of the nerves must be related to the method of distribution of the structure supplied. Whoever, therefore, discovers a new artery learns something of the distribution of nerves; and it is reasonable to suppose that the distribution and origin of the vessels depend on factors which also determine the distribution and, perhaps, the origin of the sympathetic nervous system.

Majendie(8) appreciated the relationship between the nervous system and the blood vessels when he wrote:

A general law of economy is that no organ continues to act without receiving arterial blood; from this results, that all the other functions are dependent on the circulation; but the circulation, in its turn, cannot continue without the respiration by which the arterial blood is formed, and without the action of the nervous system, which has a great influence upon the rapidity of the flowing of the blood, and upon its distribution in the organs.... Probably the distribution of the filaments of the great sympathetic on the sides of the arteries has some important use; but this is entirely unknown; we have received no light on this point by experiment.

John Hilton, many years later, drew attention to the distribution of the vessels in their relation to the function of the part supplied. He could see a clear relationship between the distribution of the internal maxillary artery and the function of mastication; and between the distribution of various arteries and such functions as respiration, deglutition and gastric secretion. He felt that, "the disposition on the part of anatomists to think and to teach that nerves are distributed with designed accuracy, but that there is very little design in the distribution of the arteries" was wrong.

The work of Beevor on the blood supply of the forebrain and that of Stopford on the blood supply of the hindbrain lend strong support to Hilton's views. The variations in point of origin of the vessels in the hindbrain at first sight appear to negative the functional interpretation; but the clear cut delineation of the hypoglossal nucleus on the injection of the anterior spinal artery demands some more logical explanation than the mechanical forces due to the heart beat; more especially so, when we know that in all probability this vessel was laid down and distributed before the advent of the circulation.

In the Orang it will be seen that the gross distribution of the cortical vessels, as far as could be determined without seriously injuring the specimen, almost as accurately surveys the functional regions of the cerebrum as the methods of Elliot Smith and Brodmann.

The subject will be dealt with under two heads:

I. The gross anatomy of the blood vessels of the brain of the Orang-utan.

II. The interpretation of variations and the relationship between blood vascular distribution and functional systems.

The material used in the investigation consisted of one Orang brain in which the arteries were well injected, and of the hindbrains of seven other Orangs in which the vessels were not injected, but in which many important features could be determined.

PART I

THE GROSS ANATOMY OF THE VESSELS OF THE BRAIN OF THE ORANG-UTAN

The Vertebral Artery

Pl. I, fig. 1 shows the level at which the vertebral arteries were severed; below this level no information is obtainable in any of the specimens. The artery is placed ventral to the rootlets of the hypoglossal nerve and ends at the level of the lower border of the olivary eminence by joining with its fellow to form the basilar artery. In all the specimens this level of origin of the basilar artery is found, whereas in the large number of human brains examined by Stopford such a low level or origin was found in only one case, although in five others it was situated at the mid-olivary level.

There is the same tendency to inequality in size as one finds in man. Of the eight specimens, in five cases the left artery was larger than the right; in one the right was larger than the left, and in the remaining two the vessels were equal in size.

The Branches of the Vertebral Artery

The branches of the vertebral artery are subject to a considerable degree of variation: and yet, the terminal branches of distribution are constant. The explanation of this apparent contradiction will be given in Part II; for the moment it will suffice to say that the branches are of two types, (1) perforating, or bulbar, branches which have a direct origin from the parent artery, and (2) longitudinal branches which give off branches of the first type to the brain stem. The branches of the second type form connecting channels between perforating or segmental vessels of the same value.

Perforating branches, whether arising directly or indirectly, are constant in their final distribution. The longitudinal channels have a variability depending on the level at which the perforating or segmental branches are used

as the stems of origin for the branches of the second order. The perforating arteries are the remains of the original segmental arteries of the body. The longitudinal arteries are intersegmental links developed to enhance the circulation of the perforating arteries.

The number and position of the perforating arteries bear a constant relation to the number and position of the longitudinal vessels.

The Perforating Branches of the Vertebral Artery

Stopford classifies these branches into upper, intermediate and lower. I have not had the opportunity of examining other than the upper set in the orang.

The upper set can be subdivided transversely into ventral, lateral and dorsal branches.

The ventral set enter the substance of the bulb medial to the rootlets of the hypoglossal nerve and are dependent for their existence upon the level of origin of the basilar and anterior spinal arteries. When the anterior spinal artery arises at "an unusually low level" Stopford finds that they are most numerous. In the orang the sites of origin of the two arteries are practically constant and in all the specimens fine perforating branches enter the antero-median fissure and the surface of the bulb as far laterally as the antero-lateral fissure. These are the perforating anterior spinal arteries which have failed to become linked up with the longitudinal anterior spinal artery. Their internal distribution will be considered with the longitudinal anterior spinal artery.

The lateral and dorsal sets of perforating branches are related to the posterior inferior cerebellar and posterior spinal arteries in the same way as the anterior set is related to the anterior spinal artery. They will be dealt with when their parent arteries are considered.

THE LONGITUDINAL BRANCHES OF THE VERTEBRAL ARTERY

The Anterior Spinal Artery

The level of origin of this artery is fairly constant (fig. 2). In four cases, the contribution from each vertebral artery is given off symmetrically, and, after a series of transverse anastomoses, the median artery is formed. In the injected specimen the left contribution does not appear to join the median trunk. In one case the left branch is undoubtedly absent, and in the remainder the condition could not be determined with certainty. From an examination of this artery in man and in the orang, it is evident that it is a longitudinal anastomosis between ventral perforating branches. The stem of origin from the vertebral artery has the same value as the so-called reinforcing branches given to it at a lower level. Any variability is due to the choice of stem connecting it with the vertebral artery. It will be shown that the same explanation accounts for any variability which may occur in any of the arteries supplying the somatic functions of the body.

From the similarity of the arrangement of this artery in the orang and in man, it can be assumed that the internal distribution would be the same. The perforating anterior spinal arteries, therefore, supply median somatic and certain suprasegmental structures in the medulla oblongata, whether the branches rise from the basilar, vertebral or longitudinal anterior spinal artery. There is no anastomotic invasion of the territories supplied by the lateral and dorsal systems. The longitudinal anterior spinal artery is thus a channel connecting segmental perforating vessels of the same function.

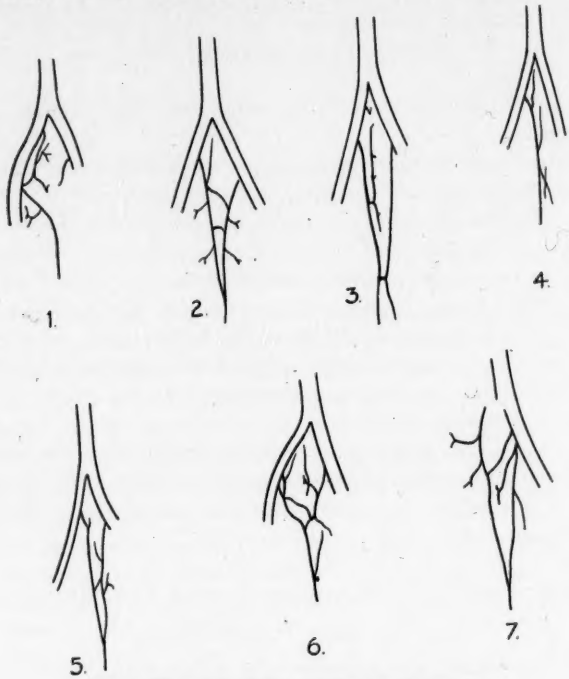

Fig. 2. The origin of the anterior spinal artery.

The Posterior Inferior Cerebellar Artery

This vessel is absent in the injected specimen. Its cerebellar supply is taken over by the anterior inferior cerebellar artery. In specimen, No 2 (Pl. I, fig. 3), the posterior inferior cerebellar artery arises from the vertebral on both sides and runs a course which is described as normal in the human brain by Stopford. It turns round the lower border of the pyramid and passes superiorly and laterally through the rootlets of the hypoglossal nerve to reach a point a few millimetres below the lower margin of the pons Varolii. In this part of its course it lies anterior to the rootlets of the vagus and glossopharyngeal nerves. It now turns back on its course, forming a well-marked curve, and descends

posterior to the vagus and glossopharyngeal rootlets, inclining at the same time towards the restiform body, to reach the region of the calamus scriptorius. It here gives off a branch which I take to be the posterior spinal artery and then proceeds to its cerebellar distribution.

For descriptive purposes the artery may be regarded as being composed of three portions:

1. A portion from its origin to the lower border of the pons Varolii. This portion passes through the hypoglossal rootlets and lies anterior to the vagus and glossopharyngeal.

2. A portion from the lower border of the pons Varolii to the point at which the posterior spinal artery is given off.

3. A portion distributed to the cerebellum.

In those cases in which the artery is said to be absent, a branch of the vertebral can always be found arising from the same site as that from which the normal posterior inferior cerebellar artery arises. This branch passes through the rootlets of the hypoglossal nerve. It gives off lateral perforating branches to the medulla, and terminates in dorsal perforating branches entering the substance of the medulla dorsal to the vagus and glossopharyngeal rootlets. It occasionally gives origin to the posterior spinal artery. It fails, however, to form the well-marked loop, and as a rule gives no branches to the cerebellum. In such cases the third part of the posterior inferior cerebellar artery is replaced by the anterior inferior cerebellar artery. Such is the condition in the injected specimen.

The lateral perforating arteries are branches of the vertebral in those cases in which the posterior inferior cerebellar artery is absent. They supply the region of the bulb between the antero-lateral and postero-lateral sulci. I propose to name this system the lateral or radicular set of perforating arteries to distinguish them from the dorsal set which supply the structures arising from the rhombic lip in the embryo. As far as I can ascertain, both the lateral and dorsal sets arise from common stems. The functional value of the three portions of the posterior inferior cerebellar artery and of the branches therefrom will be discussed in Part II.

Speaking generally, the posterior inferior cerebellar artery is subject to the same variations in distribution and origin as Stopford found in man.

The Posterior Spinal Artery

The distribution of this artery could not be determined from the specimens.

The Basilar Artery

The basilar artery (Pl. I, fig. 1) commences at the level of the lower border of the olivary eminence. This level of origin is lower than that found in man, and is the same in all the specimens examined. In every case the artery terminates at the level of the upper border of the pons Varolii. It therefore appears to be longer than it is in man.

Branches

The branches are perforating, or pontine, anterior inferior cerebellar, internal auditory, superior cerebellar and posterior cerebral.

The perforating or pontine branches are ventral, lateral and dorsal, and have corresponding areas of supply to the same systems of the vertebral artery.

The Ventral Pontine, or Anterior Spinal Perforating Branches

These vessels are clearly seen in the injected specimen. They arise from the basilar artery throughout its extent; and, as Stopford describes in man, they are more numerous cranially and caudally. From his injections it is clear that their area of distribution is continuous with the area injected by the longitudinal anterior spinal and ventral perforating branches of the vertebral artery; in other words, these branches are serially homologous with the anterior spinal perforating arteries in the medulla and spinal cord.

The Lateral and Dorsal Perforating Branches

These two systems are dealt with together for they arise by common stem branches from the basilar artery. We have seen that the anterior spinal artery is a longitudinal vessel within the area of the ventral perforating branches, and I have indicated that similar longitudinal channels occur within the other somatic systems. The posterior spinal artery is such a channel within the area of the rhombic or dorsal system, as also is the free anastomosis between the cerebellar arteries on the cerebellum. The anterior branch of the posterior spinal artery, lying ventral to the postero-lateral sulcus in the spinal cord, is such a channel in the area of the radicular or lateral set of perforating branches. These longitudinal anastomoses connect with the vertebral and basilar arteries through stem branches common to both systems: so that, whereas the ventral system is distinct, there is free communication between the radicular and rhombic systems.

I have traced the transverse, or stem, branches of the basilar artery and find that the usual description of three cerebellar arteries is too schematic. Any of the branches may supply the cerebellum, but certain branches predominate, and these are named in accordance with the level at which the stem branch is selected. A glance at Pl. I, fig. 1, makes it clear that transverse branches have been so selected. The level of origin of the anterior inferior cerebellar artery is not the same on the two sides, but in both cases the artery lies ventral to the abducent nerve. Stopford insists on the importance of the relation of this nerve to the cerebellar arteries. He records cases in which the artery lies dorsal to the nerve. It seems evident that, in those cases in which the artery is dorsally situated, the internal auditory, or some higher stem branch, has been selected. In fact Stopford shows that the internal auditory artery arises more frequently from the anterior inferior cerebellar artery than from the basilar.

The transverse stem branches of the basilar artery pass outwards on the surface of the pons Varolii, and, after giving branches to the substance of the pons, end in the supply of the cerebellum. They do not communicate with the ventral system. Such is the description which applies equally well to any of the transverse branches of the basilar artery or of the vertebral artery. It can be said that where the stem branch is enlarged to join the cerebellar, or rhombic, anastomotic area, it is dignified by a special name. If it arises low down it takes the name of posterior inferior cerebellar; if somewhat higher, anterior inferior cerebellar, and if higher still, the internal auditory artery is said to arise from the anterior inferior cerebellar artery. The final distribution is the same; in other words, the variability is not haphazard, but follows a definite method which will be more fully described in Part II.

Stopford's work makes a more detailed description of these vessels unnecessary.

The superior cerebellar arteries arose from the posterior cerebral artery in every case examined.

The Circle of Willis

The circle of Willis is arranged in the usual manner. The vessels which enter into its composition are equal in size and symmetrically arranged on both sides. I do not propose to describe it fully.

The Posterior Cerebral Artery

The posterior cerebral artery, formed by the division of the basilar artery, passes slightly forwards and outwards, curving sharply round the third nerve; it then passes backwards curving round the cerebral peduncle and terminates within the sulcus calcarinus (Pl. I, fig. 1, and Pl. II, fig. 4). Immediately anterior to the point where it curves anterior to the third nerve, it is joined by the posterior communicating artery.

This artery is usually described in human anatomy as ending within the calcarine fissure by dividing into parieto-occipital and calcarine branches. In this specimen there is no parieto-occipital branch; its area of distribution is taken by the anterior cerebral artery.

Branches of the Posterior Cerebral Artery

The branches are cerebellar, perforating and cortical.

The *superior cerebellar arteries* are from two to three in number on each side and pass to the surface of the cerebellum. I have not been able to determine their distribution with any accuracy.

The *perforating arteries* can be seen entering the posterior perforated spot and are arranged in medial and lateral sets. I have frequently injected these arteries in man and found their distribution so precisely arranged, that I wrote in 1920 (11):

The posterior cerebral and posterior communicating arteries are so precisely distributed in my specimens that the description given by Beevor of the

arterial supply of the optic thalmus could well have been made from my specimens.

Their internal distribution could not be determined in the orang.

The Cortical Branches (Pl. I, fig. 4, and fig. 5)

The main cortical branches were traced to their final distribution and the areas demarcated by conventional signs (fig. 5). These branches are so arranged that they mark out the functional areas already determined by Elliot Smith (9) and Brodmann (10). There are four main branches; the first two are generally named the anterior temporal branches, the third is the posterior temporal and the fourth the calcarine.

The first anterior temporal artery is small and supplies the area No. 20, or area temporalis inferior of Brodmann. The second anterior temporal branch supplies the area No. 37, or area occipito-temporalis of Brodmann. The posterior temporal artery supplies the area No. 19, or area prae-occipitalis of Brodmann, as far superiorly as the sulcus praelunatus. The final branches mark out almost exactly the striate cortex on the medial and lateral aspects of the hemisphere. It is to be remarked, however, that the extreme edge of the striate cortex bordering the sulcus lunatus is supplied by the anterior and middle cerebral arteries (Pl. II, fig. 6).

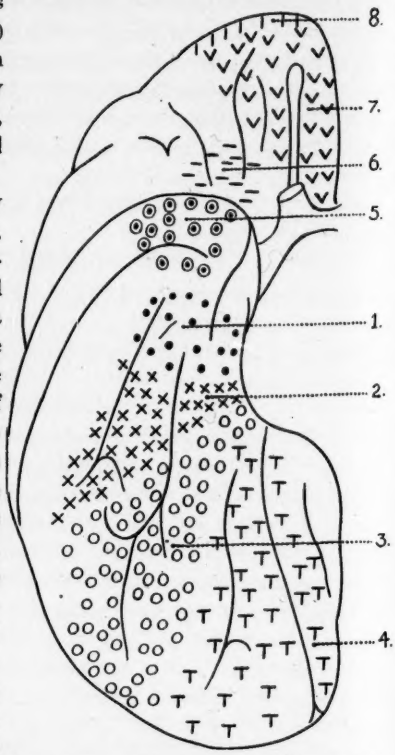

Fig. 5. Areas of distribution of cortical arteries. 1. and 2. Anterior temporal. 3. Posterior temporal. 4. Calcarine branches of the posterior cerebral artery. 5. Arteria temporalis polaris. 6. Arteria orbitalis of middle cerebral. 7. Arteria praefrontalis. 8. Arteria frontalis polaris of anterior cerebral artery.

The close correspondence between the distribution of the calcarine branches and the striate cortex has previously been noted in the human brain. The fact that the sulci, not only of the occipital region, but also of the parietal region, are so diagrammatic in the brain of the Chinese, makes the examination of the blood supply of the brain of this race of peculiar interest. I have been able to confirm the fact that the cortical supply is arranged in accordance with functional areas, and am making this the subject of another communication. The area temporalis polaris of Elliot Smith, being supplied by a distinct branch of the middle

cerebral artery in both the orang and man, accentuates the fixity of the distribution of the posterior cerebral artery.

The posterior cerebral artery is, therefore, predominantly visual. It supplies the pulvinar, the lateral geniculate body, the superior corpus quadrigeminum and the cortex concerned with the reception of visual impulses. It also supplies the anterior nucleus of the thalamus and the inferior temporal convolution.

The Anterior Cerebral Artery

It is convenient to divide this artery into two parts for the purposes of description. The first part extends from its origin from the internal carotid artery to the point at which the anterior communicating artery is formed; the second part constitutes the remainder of the artery.

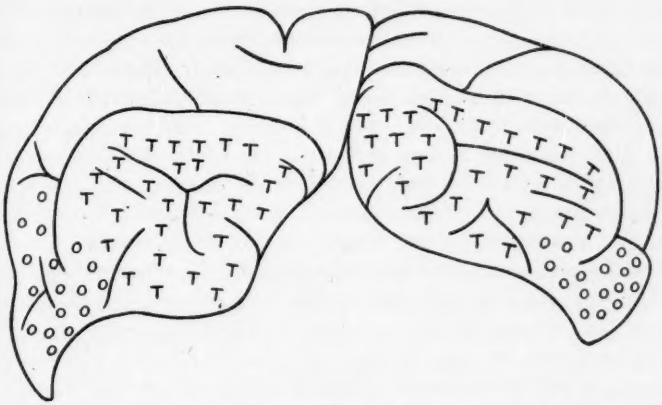

Fig. 7. The distribution of the posterior cerebral artery in the area of the striate cortex.

The distribution of the first part (fig. 7) is very closely associated with the sense of smell; it supplies that portion of the corpus striatum which lies anterior to the anterior commissure, the anterior commissure itself, the olfactory tract, the medial and lateral olfactory striae, the tuberculum olfactorium, the corpus paraterminale and the proximal part of the gyrus cinguli. I have not been able to determine the supply of the olfactory bulb.

In the specimen under consideration, the first part of the artery shows a remarkable anomaly on the left side. There is a well-marked perforation where the artery lies ventral to the medial olfactory stria: the artery divides and joins up again. Stopford records instances of perforations in the vertebral and basilar arteries, through which, in some cases, rootlets of nerves may pass. I know of no other instance of a similar condition in the anterior cerebral artery (fig. 7).

Branches of the First Part of the Anterior Cerebral Artery

It will be convenient to describe the branches of the middle cerebral artery which enter the anterior perforated spot with those of the first part of the anterior cerebral artery, since they are so closely related with each other in the supply of those areas of the brain which Elliot Smith has named the palaeostriatal and hypopallial areas. On the left side of the brain of the orang (fig. 7), there is a direct inosculation between the recurrent branch of the anterior cerebral artery and the branch of the middle cerebral artery which gives off the striate arteries to the site of the erased endorhinal fissure. The usual condition is seen on the right side where the striatal branches of the two arteries are separate from one another. Since these arteries are of such clinical and morphological importance, and since the condition in the orang is so similar to that in man, I hope I may be allowed a short digression to discuss their disposition in man. Fig. 7 will then suffice to describe the specimen.

As far as their internal distribution is concerned the work of Beevor is so complete that, with the exception of the blood supply of the claustrum, there is nothing to add to his original paper. I have confirmed all his observations.

Duret's account of the gross anatomy of these vessels has been the basis for most subsequent description, and continued repetition has detracted from the accuracy of his own description. Charcot, forming his conclusions on cerebral haemorrhage on Duret's work, laid the foundation for the accepted belief that, "the arteries of the central system, at their origin, are directed perpendicularly to the main trunk." John Hunter's observations, however, referring to the angles at which the vessels arise, are more accurate:

> I have already observed that the angles at which the branches of an artery arise may either retard or allow a freer motion of the blood; but nature appears to have taken still more care in retarding the blood's motion when velocity might do mischief. She seems also to have taken more care about the blood's motion in some parts than in others; as for example, in the brain, a part which cannot bear the same irregularity, in quantity or velocity of the blood, as many parts of the body.

The arteries which pass through the anterior perforated space belong to two groups:

1. Those which enter along the site of the erased endorhinal fissure; and
2. Those which enter posterior to the fissure.

There are three different sets of arteries belonging to the first group. Two of these arise from the middle cerebral artery, or from one of its branches, and one from the recurrent branch of the anterior cerebral artery. The first set which arise from the middle cerebral artery are arranged in linear order along the site of the endorhinal fissure; the anterior cerebral group lies anterior to and parallel with them. The third set arises from the middle cerebral or one of its branches, well lateral to the anterior perforated space; these vessels then return to be concentrated at the angle of the space in a well-marked bunch.

In the orang, figured, the first two sets of branches to the site of the endorhinal fissure, appear to arise in common from the recurrent branch of the anterior cerebral artery which has inosculated with the branch of the middle cerebral artery.

The anterior cerebral artery supplies the remaining branches which enter the anterior perforated space. These are:

1. Small branches which supply the trigonum olfactorium;

2. One large branch which enters immediately laterally to the optic tract and probably supplies the caudate nucleus.

I described these arteries in 1920, and at that time did not know that H. F. Aitken had published in 1909, "A Report on the Circulation of the lobar ganglia," in which the arteries which are named above were fully described. This report is one of the most important contributions on the subject.

The claustral arteries are given off in series with the lateral striate arteries; they are separate and distinct end arteries which perforate the lower part of the insula and pass to the claustrum.

In fig. 6 of Beevor's paper, the internal distribution of the arteries just enumerated shows a constant relation to the anterior commissure. The nucleus caudatus, anterior to the commissure, is supplied by the perforating branches of the anterior cerebral artery. The area situated lateral and postero-lateral to the commissure is supplied by the middle cerebral artery, outside which lies the claustrum supplied by its own vessels. Finally, the area posterior to the commissure, consisting of a portion of the lenticular nucleus, the internal capsule and the thalamus, is supplied by three vessels—the anterior choroidal, the posterior communicating and the posterior cerebral arteries.

From the work of Elliot Smith on this difficult region we are enabled to gain an insight into the cause of this multiplicity and yet constancy of its blood supply. In comparison with the primitive mammalia, the cortex and basal nuclei in man have increased enormously, whilst the areas related to the primitive sense of smell have become relatively reduced; and yet, the primitive vessels to these areas still retain their individuality.

The Second Part of the Anterior Cerebral Artery

The second part of the anterior cerebral artery (fig. 8, Pl. III, figs. 9 and 10) is entirely confined to the supply of the cortex. From the point at which it is joined by the anterior communicating artery it passes into the great longitudinal fissure; turning round the genu of the corpus callosum it lies closely applied to that structure as far as the splenium and then turns abruptly upwards for a short distance to pass into the parieto-occipital fissure. The second part of the anterior cerebral artery is of great interest for the areas supplied by its individual branches approximate very closely to the areas which have been defined by other methods.

The first branch is the medial orbital branch of human anatomy. Its exact area of supply is the area praefrontalis of Elliot Smith. The artery arises

immediately anterior to the recurrent branch which supplies the gyrus subcallosus; it passes to the orbital region of the frontal lobe by passing dorsal to the olfactory tract. It gives branches to the medial surface of the hemisphere as far as the sulcus subrostralis. On the orbital surface its supply is limited by the sulcus orbitalis. Its area of distribution exactly corresponds with area No. 11 of Brodmann.

Cunningham's text book describes this branch as supplying the medial orbital gyrus, the gyrus rectus and the olfactory bulb. In the Orang-utan the bulb is missing, but I am inclined to the opinion that the olfactory bulb is supplied by the recurrent branch of the anterior cerebral artery. These branches have, however, been torn in the specimen with the olfactory tract.

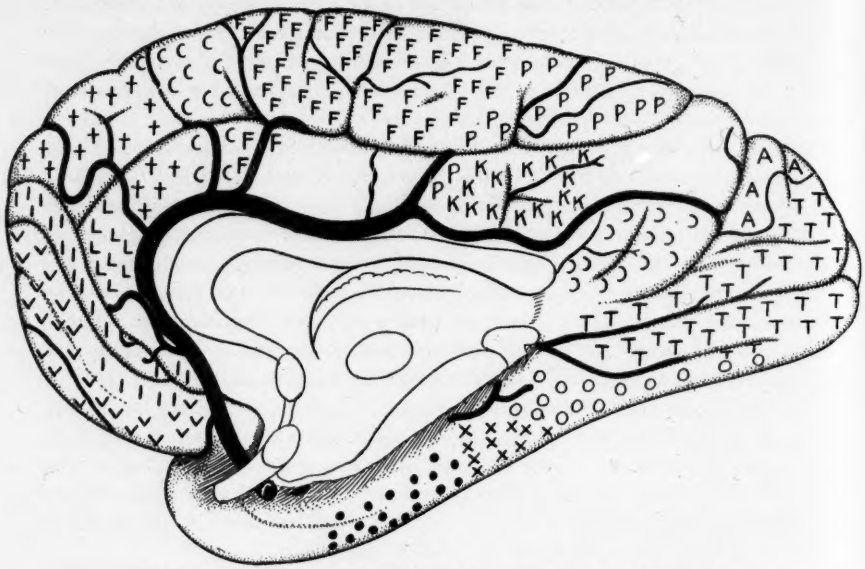

Fig. 8. The distribution of the right anterior cerebral artery in the orang.

If fig. 585 in Cunningham's text book is referred to, this artery will be found to supply the area marked with green dots. The area orbitalis is limited by a distinct branch of the middle cerebral artery.

The second branch is the anterior medial frontal artery. The area of distribution is the area fronto-polaris of Elliot Smith. This area lies between the sulcus subrostralis and the sulcus rostralis. The sulcus rostralis is a deep operculated sulcus in the brain of the orang and extends to the lower part of the superior frontal gyrus on the lateral surface of the hemisphere. The distribution of the artery extends on to the lateral surface and coincides with the area fronto-polaris. I will, therefore, name this the arteria fronto-polaris.

The third branch is included with the second in most text books as anterior

medial frontal. On both sides in the specimen the third branch is distinct, and supplies the anterior frontal area of Elliot Smith.

The intermediate and posterior medial frontal branches supply the superior frontal and paracentral gyri respectively, but it is not possible to dogmatise too closely in the specimen. Besides these named branches, there are separate branches supplying the posterior part of the gyrus cinguli and the area parasplenialis. The more exact determination of the areas of supply of the different vessels must be investigated on a larger series of brains; and I now engaged in that investigation on the blood supply of the Chinese brain.

A full description of the distribution of the middle cerebral artery is not possible without causing considerable damage to the specimen. For this reason, the opinion that the cortical supply is related to functional areas, can only be regarded as a working hypothesis until more extended observations have been made.

Pl. IV, fig. 11, shows the cortical distribution of this artery.

PART II

THE INTERPRETATION OF VARIATION IN ARTERIAL DISTRIBUTION

The variations which occur in the vessels of the brain of man can only be adequately explained by a critical examination of the development and subsequent distribution of the arteries of the body.

The development takes place in two stages; firstly, a segmental stage in which the segmental character of the body is most clearly seen; and, secondly, an intersegmental stage in which the transformation of the body into an intersegmental and suprasegmental organism leaves its impress on the vascular system as clearly as it does on the nervous and muscular systems.

The First or Segmental Stage in Arterial Development

The final distribution of the arteries of the body is governed by the pattern which is laid down before the establishment of the circulation. The origin of the primitive blood vessels from angioblastic cells, derived from the mesenchyme, has been established by Miss Sabin (13). She has demonstrated that the first vessels to arise in the embryo appear before the circulation of the blood is established. This had been suspected since the time of John Hunter who says:

> The vessels are probably the very first active parts in the system, for we find them in action before they have formed themselves into a heart, and in such a state of parts we find them the only part that has any strength, while the other parts are only preparing for action.

She has further demonstrated that the heart beats for a considerable time before the circulation begins.

Stockard (14), Knower (15), Chapman (16) and others have attempted to

determine the effect of the removal of the heart on the developing circulation. Stockard found in Fundulus embryos, chemically treated, that although there had never been a heart beat, the aorta developed into a vessel of considerable size. He, furthermore, established the law that an arrest in development at a particular time, from whatever cause, had the effect of causing malformations of definite type depending on the time of arrest. From this it is apparent that any experiment, in which the heart is removed, must be examined, not only from the point of view of the immediate mechanical effect on the animal, but also from the point of view of arrests in development produced by the mutilation itself.

Even assuming, however, that no other effect is produced than that consequent upon the loss of the mechanical forces produced by the heart's action, these experiments abundantly prove that the development of the segmental vessels has no relation to the mechanical forces due to the heart's action. Knower found that, "even after extensive operation, involving much of the neighbouring tissues, before the heart is clearly differentiated, the aorta, the large veins and the segmental vessels are laid down." Chapman used the experiment to prove that the circulation is laid down in accordance with the postulates of Thoma. It is difficult to follow his line of reasoning which led him to the conclusion that whilst certain vessels are developed by "hereditary factors," the remainder are dependent on the mechanical forces derived from the heart's action. He admits, however, that by the time the circulation begins, the embryo has a primitive but complete system of blood vessels, and that, "if the time of circulation is delayed the further development of the vascular systen is not inhibited."

There is no question of any other mechanical factors concerned in the development of the circulation than those produced by the heart beat. This is in general agreement with the view of those who would attribute the further development of the circulation to mechanical factors. Any theory which is put forward to explain the vascular distribution should stand the test of explaining the whole circulation. If the mechanical force of the heart beat is eliminated, those who look to the postulates of Thoma for their explanation must fall back on such vague terms as "hereditary factors" to account for it.

We are, however, not dealing with the circulation of embryos which have been multiplied, but with normal living embryos whose blood vessels are distributed for the purpose of supplying organic structures. Neither are we dealing with arteries merely as arteries separated from organs, but with the development of arteries which can be traced to the organs which they supply—in other words, with distribution.

The arteries will, therefore, be considered in the order of their appearance and in relation to the order of appearance of the organs supplied by them.

The hypothesis which it is my purpose to prove is:

That the segmental arteries of the body are developed *in situ* in relationship with the organ which they are to supply; that these arteries are phylo-

genetically and ontogenetically stable; that having been developed to supply an organ, they supply that organ throughout life; and, finally, that when a primitive functional area develops greater function, the vessels supplying the greater functioning area are derived from those supplying the primitive area.

It is apparent that the proof of this hypothesis must lead to the abandonment of the vicious doctrine that muscles, nerves and arteries develop independently of one another by a process of "self-differentiation."

The first arteries to appear in the body, apart from the extra-embryonic vessels, are segmental in character and are distributed in accordance with the functional needs of the body as a segmental structure. If gill clefts were present in each segment, there would be no need for either a heart or an aorta. The segmental arteries are sufficient for the needs of a segmental organism. The functions of the body are, however, threefold: segmental, intersegmental and suprasegmental. There is the suprasegmental heart, the intersegmental vessels, of which the most striking is the aorta, and the segmental vessels. In the nervous system there is the segmental reflex arc, governed by intersegmental and suprasegmental mechanisms. The muscles are arranged, first segmentally, then intersegmentally, and finally suprasegmentally. The musculature of the arm is designed to respond to suprasegmental cerebral stimuli—the vertebral and subclavian arteries arise from the same segment.

The segmental pattern of the vessels of the embryo is fairly well established: it is represented diagramatically in Cunningham's *Text Book of Anatomy*, in Keibel and Mall's *Manual of Human Embryology* (17) and in other works. The vessels are arranged in three groups: somatic, genito-urinary and visceral. The visceral group is included for descriptive purpose only, since there is no evidence that the gut is segmentally arranged. The arteries of these three groups belong to three main functional systems, in which the main artery to each system is an artery of functional value and an end artery—that is, there is no arterial anastomosis between the groups.

The end artery with which this paper is particularly concerned is the segmental somatic artery. Its area of supply is the area of the segmental reflex arc. As a whole it supplies the skin, or receptors, the sensory ganglion, the segmental intercalated region of the neural tube, the motor ganglion cells, or effectors, and finally the muscles, or expressors.

But whilst the whole is a functional system, distinct from the genito-urinary and visceral systems, so also each component of it is a functional system and the artery to each component is an end artery.

THE FUNCTIONAL UNITS OF THE SEGMENTAL SOMATIC ARTERY

The Effector, or Perforating Anterior Spinal Artery

Professor R. A. Dart and I (5) called attention to this artery in 1922. Its position and relations are the same in all embryos. It is depicted by Hensen, His and most writers on the origin of the peripheral nervous system. It is situated immediately internal to the motor ganglion cells of the anterior

horn. If sections of the medullary tube, impregnated by Cajal's method, are examined at this stage, the line which is taken by this artery will be found to be the line taken by the fibres of the anterior commissure which is developing at the same time (Hertwig, "Embryology of Vertebrates," Vol. IV, figs. 153 and 154)(18). Obviously the stage of development is later than the pure segmented stage of the embryo, for already intercalated or intersegmental fibres have developed sufficiently to become impregnated. It must, therefore, be determined how this vessel came into this position which is retained throughout life. Obviously it did not arise within the medullary tube; and, therefore, the angioblastic cord must have migrated in from the outside by an active process, or it must have become circumvested by the encroaching external layer of the medullary tube by a passive process of intrusion.

The difficulties of accepting the first supposition are that:

1. Similar active migrations are unknown in the body in the case of the blood vessels, or at least have not been proved:

2. The constancy of the position of the artery: and,

3. The absence of any evidence that the external limiting membrane is the same structure at different ages of development.

The second supposition is the more probable, but its acceptance demands a reconsideration of the current views on nerve development.

The somatic segmental artery arises before the circulation is established, at a time when the medullary tube is segmented and when its marginal layer is defined by the so-called external limiting membrane, when nerve fibres are not impregnatable, when the cells of the medullary tube are undifferentiated, and when the dorsal element of the somatic segmental artery is external to the medullary tube with evidence of commencing development of branches (Keibel and Mall, fig. 439). So that whichever supposition is correct the rudiments of the anterior spinal artery are outside the medullary tube. In the next stage (see Hertwig, fig. 154), a great change has taken place in all parts of the embryo. The development of an entirely new system of arteries has taken place and the heart has begun to function. The new system of arteries comprises the longitudinal intersegmental arteries—the aorta, the vertebral, the longitudinal anterior spinal artery and others. The advent of intersegmental function has been signalled by a re-arrangement of the myotomic and lateral muscle sheets, producing an intersegmental arrangement of the vessels of the trunk and limbs. The nervous system has responded by the development of impregnatable neurofibrillae arising from the mantle layer of the medullary tube. These fibres, both commissural and intersegmental, have become impregnated in the region which is recognised as the marginal layer of the earlier stage. It is here also that the anterior spinal artery is seen. The motor ganglion cells lie external to the artery and to the position of the external limiting membrane of the earlier stage as well as to the impregnated fibres belonging to the intercalated neurones. Clearly the artery has not penetrated the external limiting membrane of the segmented stage.

This interpretation infers that the external limiting membrane of the medullary tube is not a fixed structural entity, but that with each succeeding stage in development the so-called external limiting membrane occupies a more lateral position, being as it were re-formed, not expanded. This accounts for the fact that the impregnated cells of motor type are always external to the anterior spinal artery in the medullary tube. In the further growth of the embryo these relations are maintained. In support of the hypothesis that the motor cells and anterior spinal artery have become absorbed into the neural tube, as an expression of the advent of intersegmental function, we find that the radicular and rhombic arteries have likewise become absorbed into the dorsal region of the medullary tube, together with the dorsal columns of the cord, which are clearly of extra-neural origin. It is in the dorsal region that the limits and form of the earlier medullary tube can be most plainly seen. There can be no doubt that, if the sensory ganglia had become included in the medullary tube (as is perhaps the case with a portion of the fifth nerve), the medullary tube origin of all sensory nerve cells would have become the subject of a scientific dogma. The present teaching of nerve development denies to nerve elements that which must be granted to the vascular elements, that is, absorption from the outside.

A digression is here necessary, for if the anterior spinal artery is developed as a part of the reflex mechanism, and, if it does arise *in situ* with the anterior horn cells—as the evidence would tend to show—then the conclusions arrived at by Harrison (19) from an experimental study of the tissues of tadpoles must be abandoned. The present doctrines of development are founded on the conception that the tissues of the body develop by a process of "self-differentiation." A mental picture of disconnected units ultimately uniting to produce functional systems dominates the teachings of anatomy. But if it is accepted that the reflex mechanism develops as a whole, in which each of the component parts is intimately linked together from the beginning, then it cannot be accepted that the nerve and muscle develop independently without anatomical connection.

The brilliance of the operative procedure of Harrison is beyond question. A repetition of his experiments would in all probability lead to the same results; but the conclusions which have been deduced therefrom are open to other interpretations. His two classical experiments, which would at first sight appear to negative the idea of continuity of the structural elements involved in a functional mechanism are:

1. The experiment which proves that a nerve cell grown in a culture medium behaves in a specific manner: and,

2. The experiment which is designed to prove that, when a muscle is separated from its nerve, the muscle is capable of independent development.

Graham Kerr (20) has brought a considerable amount of evidence in disproof of the theory that the medullary tube and myotome are not in organic continuity. He has discussed the question fully in his textbook of embryology, and

having examined his specimens of Lepidosiren, there is no other conclusion to be arrived at than that there is structural continuity between the myotome and the muscle. But it is an interesting fact, which has been missed by the contestants in this discussion, that Harrison's experiment actually proves the opposite from that which he says it does. He has shown that there can be no amoeboid movement of a nerve cell unless there be a bridge for the protoplasm to use. His experiment is of great value, for it gives information of the behaviour of a nerve cell—or perhaps only a part of a nerve cell—in a fluid medium, and in a medium in which a supporting tissue is present. Unfortunately it fails to give the information required. What is the behaviour of a nerve cell in the body of a living normal embryo? What is the behaviour of a nerve cell which is the subject of changes consequent upon the transformation from segmental to intersegmental and suprasegmental function? Harrison's experiments fail to take into account the laws of neurobiotaxis set forth by Ariens Kappers.

In the second experiment, Harrison inserts a quill between the medullary tube and myotome at an early stage. In this experiment he severs the connection which is already in existence, although he denied this. The muscles separated show the reaction of degeneration as far as one can tell. Unfortunately we have no evidence of the appearance of a degenerating nerve in a tadpole, but Harrison says that the muscle develops normally and that *it does not respond to either mechanical or electrical stimulation.*

To resume. The somatic segmental artery responds to the myotomic differentiation by providing the perforating anterior spinal artery. Where this artery is injected by the method of Beevor the picture produced is diagrammatic. The anterior horn cells are invariably supplied. Similarly Stopford says, "Invariably the trigonum hypoglossi was accurately defined by the stain of the injection."

The Sensory Arteries of the Segment

There appears to be a distinct branch of supply to the sensory ganglia. In the medullary tube itself, two systems of perforating arteries can be distinguished in the embryo. One system is distributed to the region posterior to the entrance of the dorsal nerve roots, and one system anterior to them. The first system is the one I have referred to as the rhombic system of perforating arteries; the second system is the radicular system. There is no apparent anastomosis between the areas concerned. It is apparent that the classification here put forward might be somewhat schematic, and that Stopford is correct in issuing a warning against such a threefold classification. He says that:

> The subject is somewhat controversial, and often rendered obscure by many writers in their endeavour to divide the cord into three districts—first the part supplied by the anterior system, secondly a part supplied by the posterior, and lastly the part supplied by both.

In justification of such a schematic rendering, however, I must refer to his own pictures (figs. 7, 8, 12 and 19). There can be no question of the definite entity of vessels which would so clearly define the hypoglossal and vagal triangles (both of which observations I have personally confirmed), and of vessels which should so separate the posterior columns and their nuclei. But with the lateral somatic motor nucleus supplied, apparently by the radicular system, it is clear that the establishment of the hypothesis put forward here requires even more discriminating work than that which has been done by Stopford.

The rhombic system of vessels supplies the structures derived from the rhombic lip in the embryo; and the radicular system supplies the intercalated nuclei, including the vagal nuclei, amongst other structures in the medullary tube.

The Muscular Branches of the Somatic Segmental Artery

Leaving out of account the arteries which supply the bones and supporting structures, the remaining branches of the segmental artery are muscular, supplying both dorsal and lateral musculature. The best example of the lateral somatic supply is seen in the vessels of the forelimb. This has been investigated by Woollard (21) and others. Whilst the pure segmental supply cannot be ascertained with certainty by the method of injection, the first stage described by Woollard is so early in the intersegmental stage that the assumption is justified that the segmental arteries of the limb are derived from the same segments as the nerves and muscles. Woollard lays stress on the fact that there is no variability at this stage.

It can, therefore, be said that the arteries of the animal in the segmental stage are constant in distribution. They are definitely distributed in relation to the function of the part supplied and are end arteries within that area. They develop synchronously with the structures which they supply, and arise *in sutu* from angioblastic cells. Furthermore, at this stage the distribution can in no way be attributed to mechanical forces.

Before proceeding to the description of the changes which take place on the advent of intersegmental function, it is necessary to make a clear distinction between two definite elements of each functional segmental artery; for it is clear that if each artery is an end artery within its own area, then no intersegmental circulation can be established. The two elements are the stem of origin and the terminal portion of distribution.

The Establishment of the Intersegmental Circulation

"The establishment of the intersegmental circulation is brought about by longitudinal anastomosis between stem arteries of equal functional value." The terminal portions remain distinct and supply the area to which they were originally allotted. Any accession of function produces arteries for its supply from the capillary network distributed within the area of the function from which the new function arose. The proof of this hypothesis disposes of the

postulates of Thoma, for the definitive circulation is prefigured in the distribution which is laid down before the heart begins to beat.

The attention of embryologists has been unduly attracted to the vessels which are prominent in the adult, with the result that the importance of the terminal vessels to the organs has been lost sight of. The fact that the developing longitudinal vessels arise from stem arteries of the same value, permits some stems to be done away with. The efficiency of the circulation to the terminal segmental portions can thereby be assured; and, moreover, the blood can be distributed in response to intersegmental rather than to segmental stimuli. This method of opening up new channels allows of a certain choice of route, but the final destination remains the same. Every variation in vascular distribution can be thus explained. The variation is, however, more apparent than real, since every longitudinal vessel must consist of a stem artery as its commencement and the longitudinal anastomosis within the function of that stem. The direction of the blood stream, or the distribution of the vessels, is governed by the direction of the functional development.

Longitudinal channels arising in terminal functional areas must be entirely confined to the area of that function. Herein lies the explanation of the longitudinal anterior spinal artery and of the longitudinal radicular and rhombic channels. They are the terminal anastomotic channels in the terminal areas of function of the somatic segmental reflex.

The injection of the longitudinal anterior spinal artery reveals the blood supply of the median somatic motor nuclei. The variability of its origin from the vertebral artery is purely a question of the segmental stem which forms its commencement.

The same condition is found in the case of the lateral somatic muscular arteries of the forelimb. At the same moment as the longitudinal anastomoses are occurring elsewhere—that is, at the moment of the advent of intersegmental function—the segmental arteries of the forelimb are being connected together by a longitudinal anastomosis which passes cranially and caudally in the limb bud. This is the time when the anterior horn cells are being influenced in their position by the development of intercalated and commissural fibres.

Woollard, in describing this stage, says:

> This stage shows the dominance of the lateral branch of the seventh segmental artery so enlarged that it constitutes the main axial trunk of the forelimb bud. . . .The contributions from the other segments are disappearing.

The accuracy of his observations and the clearness of his pictures permit of a complete understanding of the changes which have occurred. The method of injection fails, however, in one important particular. It fails to distinguish the stem portion of the artery from the terminal branches of distribution. The main axial trunk of the forelimb bears the same relation to the seventh segmental artery as the vertebral artery does. It would not be correct to say that the dorsal branch of the seventh segmental artery is so enlarged that it forms

the main trunk of the vertebral artery. The only portion of the vertebral artery which is constituted by the seventh segmental artery is the stem of origin; the same is the case with the main axial trunk of the forelimb. It is the proximal or stem portions of the fifth, sixth, eighth and ninth segmentals which disappear, not, as Woollard states, "the contributions from these segments," for the final vessels of distribution remain.

The axial trunk of the forelimb is, therefore, mainly a longitudinal vessel which is formed in a terminal functional area in the sense in which I have described. The limb artery may be said to be a functional artery for the supply of lateral somatic musculature which has been converted from segmental to intersegmental function. The forelimb is one of the important organs for the expression of willed movements determined in the cerebrum; and so it is not a matter for surprise that the same segment should be the one from which both the vertebral and subclavian arteries should arise, and that they should both develop at the same time. Congdon (22), losing sight of the development of the suprasegmental structures—particularly the cerebrum—says, "There would never be a vertebral artery did not the aorta shift caudally." Then one may ask, what would supply the higher nerve structures? It is as reasonable to say that there would never be a vertebral artery did not the head grow cranially.

The rhombic and radicular longitudinal channels are similarly anastomoses in areas of terminal function. The rhombic system supplies the structures which are derived from the rhombic lip in the embryo. The second portion of the posterior inferior cerebellar artery is a part of this channel: and thus we have the explanation of the frequent origin of the posterior spinal artery from the posterior inferior cerebellar artery.

The radicular longitudinal channel is formed ventral to the posterior nerve roots. It supplies, among other structures, the intercalated elements of the reflex arc. The first portion of the posterior inferior cerebellar artery consists of this longitudinal anastomosis with the important addition of the stem branch which connects it with the vertebral artery. The stem branch of the anterior spinal artery is a stem branch of a single functional system; the stem branch to the radicular and rhombic systems supplies at least two functions developed on the sensory side.

If we turn for a moment to the development of the aorta and its main branches this will become clear. The aorta for the greater part of its extent is the main longitudinal channel connecting up the functional arteries of each segment. It is the great intersegmental artery. Any branch which it gives off must of necessity start as a stem branch of a single functional system of segmental value and then pass to a longitudinal vessel. Starting from the point at which the vertebral leaves the subclavian artery, the commencement is the stem of the dorsal segmental artery; it must then pass to all the elements concerned in the dorsal part of the segmental reflex arc. The course of the circulation is thus established; it always passes from an area of higher function to areas of subordinate function derived from the higher function. The longi-

tudinal anastomoses take place at each point of differentiation of function. The variability of the posterior inferior cerebellar, the anterior inferior cerebellar and internal auditory arteries and their interdependence on one another has here its explanation. The commencement of any one of them is a stem of equal value, and whichever stem is used the distribution remains the same, since the stem leads to the same longitudinal channels. The free anastomosis on the surface of the cerebellum is due to the tendency of longitudinal anastomoses to take place within areas of the same function.

To summarise, the distribution of the blood is governed by the segmental pattern laid down before the advent of the intersegmental functions; and since the segmental vessels are end arteries in the sense that they do not enter into arterial anastomosis with arteries of different function, the establishment of the intersegmental circulation can only take place by the opening up of anastomoses between arteries of the same function. The direction of the circulation is thus determined, passing as a general rule from a system of higher function to a system of lower function developed from it. All the arteries of the body are laid down, therefore, in response to the functional needs of the body.

The first law of arterial distribution in the segmented embryo is: "All segmental arteries are end arteries and are distributed to areas of functional value." This must be modified for the intersegmental animal as follows: "All arteries which retain their segmental value are distributed to one area of function and are end arteries within that area; all intersegmental links take place between areas of the same function."

It follows from this that, "all arterial anastomoses in the body connect areas of similar function." "Areas of dissimilar function are connected by capillaries."

The Establishment of Commissural Circulation

A change which is quite as important to the animal is the development of commissural function. It takes place at the same time as the development of intersegmental function and impresses itself on the vascular system at the same time as it does on the nervous system. The sites at which commissures are formed are the sites of transverse anastomoses between the two sides of the body. The transverse anastomoses follow the same law as the longitudinal anastomoses; they take place between arteries of equal function. The median longitudinal anterior spinal artery is therefore both longitudinal—or intersegmental, and commissural. It takes place at the same time as the anterior commissures are being formed in the medullary tube. The main sensory decussations do not take place until the hindbrain is reached: and here where both the pyramidal and sensory decussations occur we find the basilar artery.

The Cause of the Vascular Distribution

The clue to the underlying cause of the vascular distribution is to be found in the fact that the sympathetic nervous system arises *in situ* in relation to the

organs which it supplies. The ectodermal origin of the whole of the peripheral nervous system can no longer be upheld. I do not intend to discuss here the question of the development of the peripheral nervous system; suffice it to say that the first rudiments of the sympathetic nervous system are found away from the ectoderm. Elliot Smith (9) says, "The observations of Professor J. P. Hill upon embryos of Echidna seem to suggest that in mammals these gustatory neuroblasts are derived from the entoderm." Dr Dart and I have found that certain of the gustatory neuroblasts arise from entoderm in both the elasmobranchs and the amphibians. The fact that the sympathetic nerves arise in common with the tissues they supply, means continuity of functional mechanisms from the beginning. It is the distribution of the sympathetic nervous system which governs the distribution of the blood vessels. John Hilton said that, "there is a disposition on the part of anatomists to think and to teach that nerves are distributed with designed accuracy, but that there is very little design in the distribution of the arteries." This was written half a century ago, and the disposition is still existent, for during the interval the anatomical world has been dominated by the mechanistic mind of His. Students understand full well the three germ layers in the coloured diagrams of text-books, but fail to recognise them in the embryo itself. Miss Sabin has proved beyond question that vessels are laid down before any mechanical forces are operative:

> It is thus clear that at the stage of 12 somites, when the head of the embryo contains a complete aorta and a neural system of vessels which consists of a plexus of large vessels on the forebrain and midbrain, and a single channel on the hindbrain, there is no circulation through these vessels due to the beat of the heart.

In spite of that work, the mechanical postulates of Thoma still obscure the vital living processes which are going on in the body.

One might well ask, which vessels in the body are laid down in accordance with these postulates? For the postulates of Thoma are as follows:

1. An acceleration of the current leads to an enlargement of the lumen of the vessel, and a slowing of the current leads to its narrowing and final disappearance.

2. An increase in the blood-pressure is the cause of new formation of capillaries.

3. The growth in thickness of the vessel wall depends on the tension of the wall, which in turn is dependent upon the blood-pressure and the diameter of the vessel.

The first and third postulates can have nothing whatever to do with the distribution of the vessels for they refer to vessels already laid down. That the vessel wall may, and probably does, respond to mechanical forces cannot be disputed; but if Miss Sabin is right, and there is little doubt that she is, the aorta not only forms, but also increases, in surface and thickness before the heart beats. In two-headed monsters the distribution of the vessels is in

accord with function. Are the mechanical forces the same as in normal embryos? Further, are the mechanical forces the same in elasmobranch fishes as they are in human embryos? Some other explanation must be found for blood vascular distribution. I know of no evidence for the second postulate.

Those who regard the vascular distribution as being governed by these laws have not specified the particular arteries to which they refer. This omission makes it imperative to specify the arteries of the body which are laid down in response to functional stimuli. It must also be shown that the sympathetic nerves are uniformly distributed in the same areas to prove that the distribution of the muscles, nerves and arteries are laid down in the form of operative mechanisms. The establishment of the common origin of these structures must overthrow the three germ layer theory in so far as the layers are regarded as being the originators of structures which are separated from one another in the beginning and later join together.

The cells of the myotome can be regarded as mother cells capable of specialising into neuromuscular cells of two types. The differentiation of the two types of cells leads to a further specialisation of neural and muscle cells. In the case of the neural cells supplying striped muscle there is an absorption into the medullary tube in response to intersegmental needs; in the case of the neural cells supplying the smooth muscle of the arteries, the intercalation takes place at the periphery.

Some Functional Arteries of the Body

The distribution of the arteries to the forelimb have already been discussed in referring to the work of Woollard. The limb arteries belong to the same segments as those from which the nerves and muscles arise. The exact distribution of the sympathetic nerves to the vessels has not been fully established; it is probable, however, that the main axial trunk carries only those derived from the seventh segment, whereas the remaining nerves are distributed for a variable distance in the nerve trunks before being given off to the vessels.

The functional differentiation of the axial musculature reveals a similar functional differentiation of the arterial supply. Thus we find segmentally arranged vessels supplying both the epiaxial and hypaxial musculature. The deep cervical artery is the longitudinal vessel of the musculature, reinforced by segmental branches of the vertebral artery—the artery of the segmental reflex arc. The hypaxial artery is the ascending cervical in the neck region, and below that the internal mammary artery. The arterial supply of the diaphragm reveals a definite functional distribution. The diaphragm is derived from various sources. The ventro-lateral portion is derived from the ventral longitudinal muscular sheets which also give rise to the rectus abdominis and the depressors of the hyoid bone. The artery of supply of this portion is the internal mammary artery. It is the longitudinal artery in the area of the ventral longitudinal musculature. It can be taken together with the ascending cervical

artery; in fact, the internal mammary artery frequently springs from a higher level than usual and then arises in common with the ascending cervical from the thyroid axis artery. The arterial supply of the diaphragm is closely associated with the supply of the phrenic nerve, as pointed out by Hilton. Not only is the phrenic nerve supplied by the arteria comes nervi phrenici of the internal mammary, but also by the ascending cervical artery in its upper part. The variations in the origin of the internal mammary in no way alter its distribution.

The homologies of the branchial musculature are not settled. It has been classified by some as visceral; this is a matter of little importance as far as the arterial supply is concerned, but I cannot see the logic of classifying striped musculature supplied by effector neurones of somatic type as visceral. This question has been discussed by Dart (23) and Herrick (24) and it will here suffice to say that I regard the nucleus ambiguus as being serially homologous with the lateral groups of nerve cells supplying limb musculature; in other words, I regard the limb musculature as branchial in origin. I hope to be able at a later date to differentiate the arterial supply of the nucleus ambiguus from the rest of the radicular area of supply; until this has been done, the opinion that the limb musculature is branchial in origin can only be regarded as a working hypothesis founded on the serial character of the nerve supply.

The arterial supply of the branchial musculature is precise in its distribution. It is phylogenetically and ontogenetically constant. The blood supply of the masticatory apparatus is confined to the internal maxillary artery. John Hilton speaks of this artery as the "true masticatory" artery.

The internal maxillary artery supplies the teeth, the bones from which all the masticatory muscles arise, the muscles and nerves concerned with this function. It supplies both the old and the new mandibular joints. Some branches would, at first sight, appear to have no relation with mastication, such as the middle meningeal; some of these have been dealt with by Hilton. He omitted, however, to mention the branches which it sends to the ear. The membrana tympani, developed in part from the first branchial cleft, receives its supply from it; more interesting, however, in the light of the work of D. M. S. Watson on the evolution of the ear, is the fact that the incudo-malleolar joint is supplied by the same artery. The law of phylogenetic constancy here receives remarkable confirmation.

The external maxillary artery supplies the structures derived from the second arch. It supplies the Eustachian tube, the tonsil and the muscles derived from that arch. It is surely obvious then that there is a force more potent than mere mechanical convenience which shows a distribution, so explainable on phylogenetic grounds.

Hilton says:

> Look at the arterial distribution of the blood to the soft palate, derived from several different sources. The soft palate is functionally connected with respiration, deglutition and mastication, so we ought to discover that its arteries

are derived from the trunks of those arteries which supply the face and lips, those which supply the masticatory apparatus, and the walls of the pharynx. Curiously enough, this soft palate receives six arteries, three on each side: one from the facial, the ascending palatine which seems to take a wandering course up to the soft palate; one from the ascending pharyngeal, and one from the internal maxillary, the "true" masticatory artery:...Here then is a simple piece of anatomy which shows the precision and purpose of the distribution of arteries which seem to be associated with three different functions: one in relation to respiration, associated with the muscles of the mouth derived from the facial artery; another in relation to deglutition, receiving its supply from the ascending pharyngeal artery; and a third in relation to mastication, receiving its supply from the masticatory artery.

But whereas difficulties may occur in unravelling the somatic muscular areas of the body, owing to the complex nature of the re-arrangement of the myotomic masses, the distribution of the vessels in accordance with function is more clearly indicated in dealing with the visceral and genito-urinary systems.

In the visceral tract the coeliac axis artery—the secretory artery—is distributed within the area of the secretory organs. The hepatic artery supplies the liver: the splenic artery supplies the pancreas, the spleen and the stomach in part; the gastric arteries supply the remainder of the stomach. The anastomoses between these arteries of similar function is very free, but their terminal branches of distribution appear to be end arteries. The whole of the area supplied, with the exception of the spleen, is concerned with secretion. This area terminates roughly at the duodenal papilla where the supply is taken on by the superior mesenteric artery—the artery of absorption. The excretory portion of the gut is supplied by the inferior mesenteric artery, with the exception of the area developed in association with the cloacal musculature. This area is supplied by the internal pudic artery, the precise nature of which has been referred to by Hilton.

The Functional Distribution of the Arteries of the Brain

It is here that we must turn to the work of Stopford and Beevor, the greater part of which I have personally confirmed. I have cited the precise nature of the blood supply of the various organs of the body as an introduction to the condition in the brain. Whilst in some respects the hypothesis put forward by me would appear to be clearly proved, in other respects difficulties arise. For example, the same artery which supplies the hypoglossal nucleus appears to supply also the pyramidal and other tracts; the same artery which supplies the radicular intercalated neurones supplies the lateral somatic nucleus or nucleus ambiguus; in the cerebrum the Rolandic area is supplied by two arteries, the middle and anterior cerebral; moreover, the blood supply of the cell bodies is different from that of the axone. These difficulties must be overcome before the hypothesis put forward can be set on a firm basis as a law. I feel, however, that the distribution is so regular as to warrant the opinion

that when more is known of the development of the brain tracts, it will be found that their arterial supply follows the same law as that of the other arteries of the body.

In a previous communication, I have referred to the importance of the vessels to the corpus striatum and optic thalamus, and have dealt with the precise nature of the blood supply of the brain. That work, together with the clear evidence produced by Stopford and Beevor, leaves little more to be said. It is necessary, however, to refer once more to the remarkable precision of the supply to the cortical areas of the cerebrum. It was satisfying to find that, after I had demarcated the areas of supply of the anterior and posterior cerebral arteries, these areas should so closely agree with those worked out by the methods of Elliot Smith and Brodmann. The posterior cerebral artery might well be named the artery of central vision to distinguish it from its companion the retinal artery or artery of peripheral vision, both of which tell of the method of vascular distribution.

I must here refer to the work of Elliot Smith on the forebrain. We owe to him the knowledge of the homologies of the olfactory and of the way the neopallium has been gradually formed from the interpolated region between the hippocampal and pyriform areas. The anterior cerebral artery is the great artery of the olfactory sense, including the hippocampus. The middle and posterior cerebral arteries are the arteries of the pyriform and neopallial areas. Now, since new developments of function arising out of pre-existing areas take place towards the periphery of existing vascular supplies, the greater development of the neopallium has taken place at the junctional area of the three cerebral arteries. This explains the fact that the last areas to be developed in the human brain have their counterpart in just those areas where the distribution was difficult to determine in the Orang:—in other words, the areas of junction between the three arteries. Now, since the last areas to form are those particularly concerned with the higher and more complex cerebral functions, it is not surprising that one or other of these arteries should have been found to be abnormal in the brains of the insane. Neither is it surprising that the areas which are peripheral, as far as the arterial supply is concerned, should be the first to be affected in chronic vascular lesions associated with senility.

GENERAL SUMMARY

1. The arteries of the brain of the Orang-utan closely resemble those of the human brain in both their distribution and variations.

2. The arteries of the hindbrain are perforating or segmental and longitudinal or intersegmental. The perforating arteries belong to three groups:

(i) Anterior spinal or motor arteries:

(ii) Lateral, radicular or intercalated arteries:

(iii) Posterior spinal or rhombic arteries supplying the structures derived from the rhombic lip in the embryo.

3. The arteries of the brain are developed first segmentally, then intersegmentally and suprasegmentally.

The segmental arteries are functional in their distribution, the main somatic segmental artery being the artery of the reflex arc. The intersegmental and suprasegmental arteries arise in response to intersegmental, suprasegmental and commissural demands.

4. The arteries are phylogenetically and ontogenetically stable. The intersegmental arteries are formed by anastomoses between segmental arterial stems of equal functional value; so that the direction of the circulation is in the direction of differentation of function.

5. Variations of arteries are all explainable by the choice of stem artery which is used to form the commencement of the intersegmental arteries. The intersegmental arteries are thus variable to that extent: the final distribution is constant.

6. Areas of equal functional value tend to be joined by arterial anastomoses: areas of different functional value are joined by capillary anastomoses.

7. The arteries of the body are distributed to definite functional areas. The hypothesis is put forward that this is brought about by the fact that they arise in common with the sympathetic nerve elements which supply them, and that they are therefore distributed to respond more readily to nervous stimuli.

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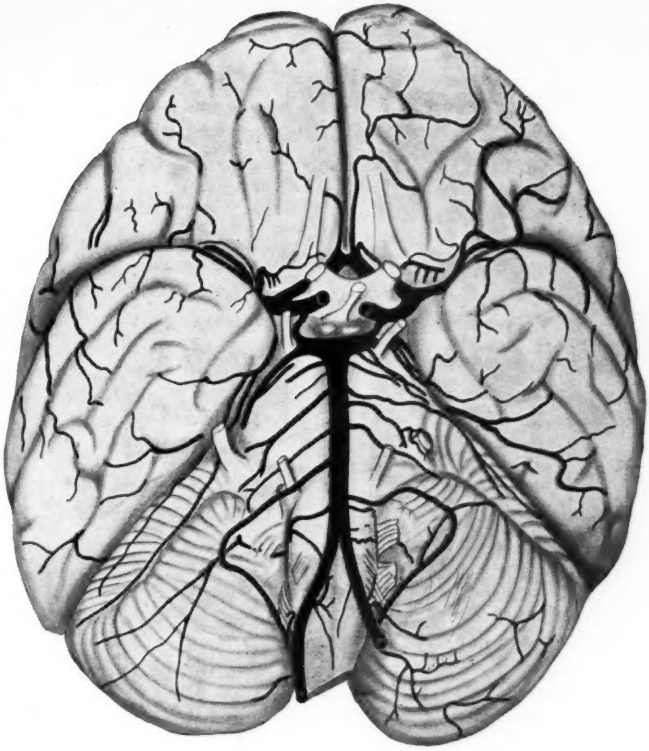

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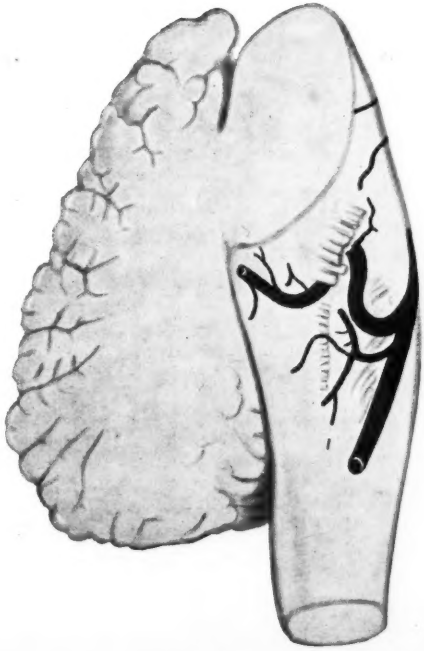

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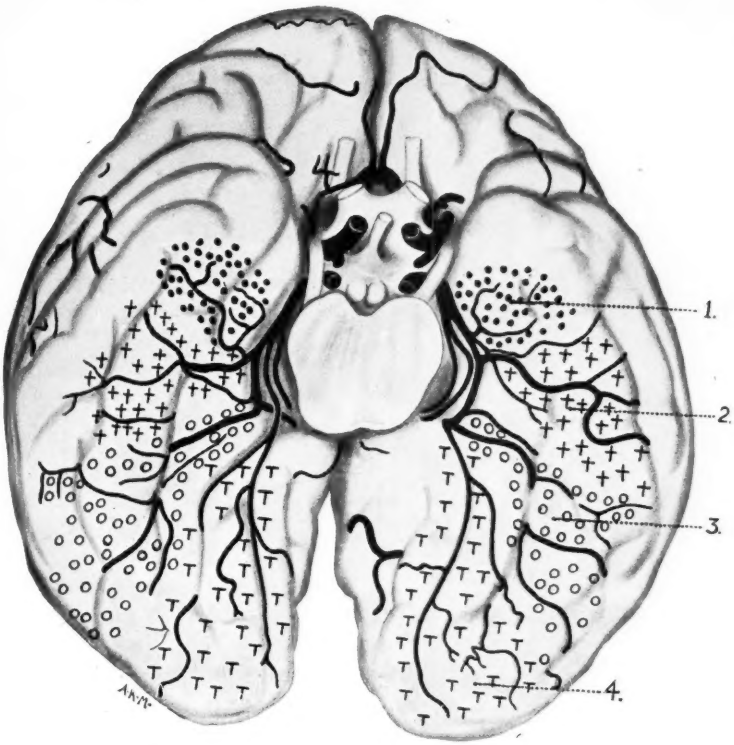

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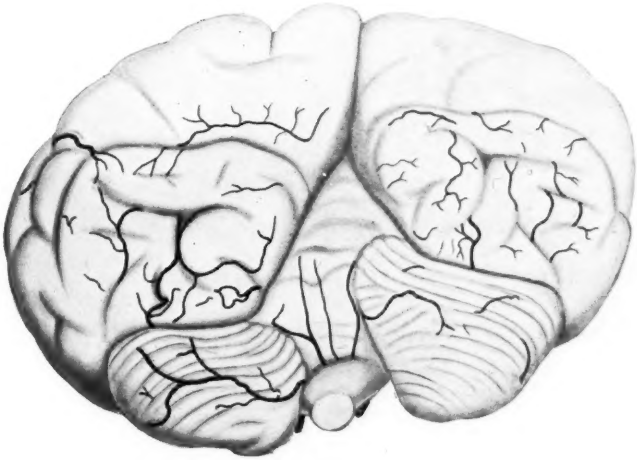

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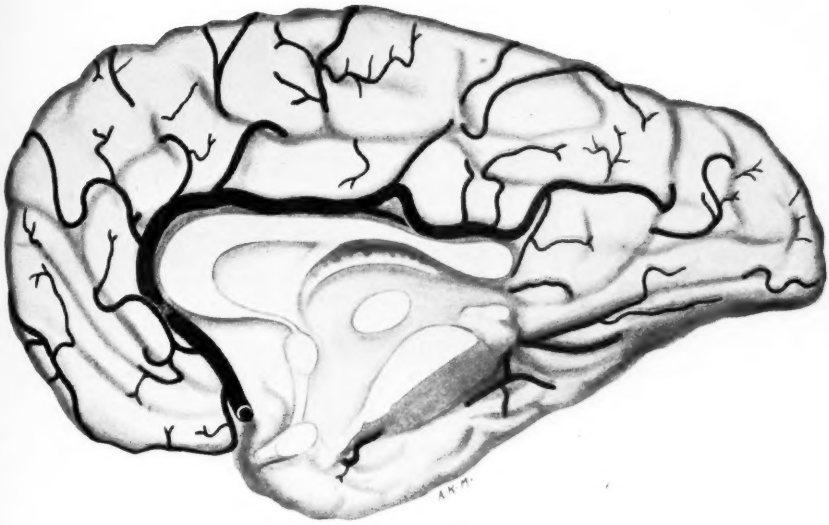

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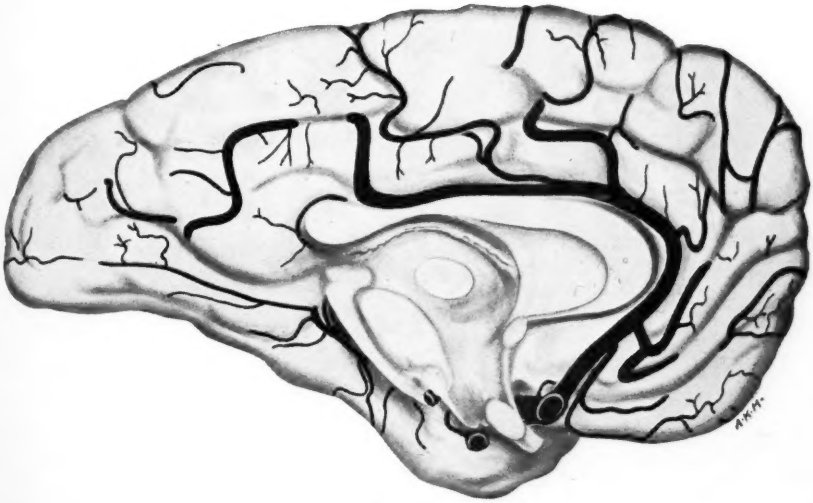

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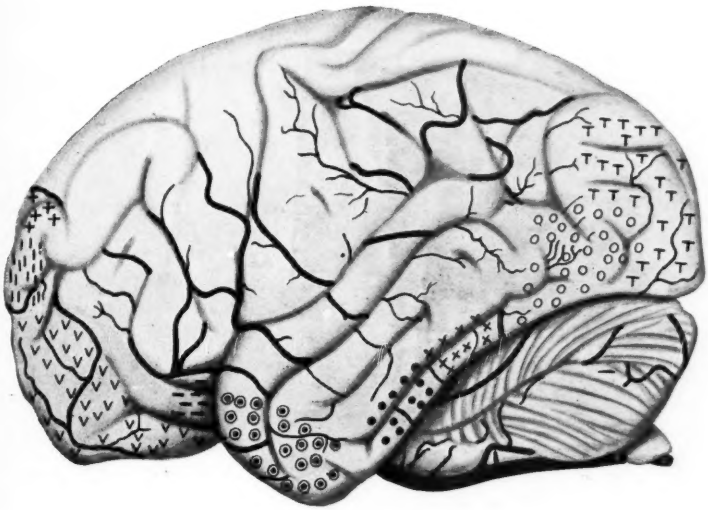

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DESCRIPTION OF FIGURES IN PLATES I–IV

Fig. 1. The arteries of the base of the brain in the Orang-utan.
Fig. 3. The course of the posterior inferior cerebellar artery in the Orang-utan.
Fig. 4. The distribution of the posterior cerebral artery in the Orang-utan. 1 and 2. Anterior temporal branches. 3. Posterior cerebral branches. 4. Calcarine branches to striate cortex.
Fig. 6. The distribution of the posterior cerebral artery in the area of the striate cortex.
Fig. 9. The areas of distribution of the right anterior and posterior cerebral arteries in the Orang.
Fig. 10. The distribution of the left anterior cerebral artery in the Orang.
Fig. 11. The distribution of the vessels on the surface of the left cerebral hemisphere in the Orang.

THE BLOOD SUPPLY TO THE PERIPHERAL NERVES OF THE SUPERIOR EXTREMITY

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The object of this research was to determine the nature of the blood supply to the nerves of the arm, both extraneural and intraneural, to find if this is at all constant, and whether it throws any light on the clinical facts relating to nerve injuries and disease, especially on the survival of nerve trunks which have been freed for operative purposes over a considerable length, and so deprived of the blood vessels going to them.

The most extensive work on the subject of the blood supply to the nerves is that of Quénu and Lejars(1), who describe the supply as being both very rich and very regular in its origin, mode of approach to, penetration of, and division in, the nerves. They lay down two laws, as follows:

(1) Each nerve trunk receives its arteries from a constant origin.
(2) They never come from only one artery, but always from multiple sources.

That the blood supply to the nerves may have importance in addition to its direct one of nourishing the nerve is shown by Zuckerkandl(2), who describes a triple collateral path in the limbs, muscular, cutaneous and nervous. Cases which occurred during the War, quoted by G. H. Makins(3), afford illustrations of this. He found that the vertical chain of vessels along the sciatic nerve always enlarges considerably when the popliteal artery is obliterated, and, in one case of an amputation for gangrene following ligature of the popliteal artery, he found a vertical vessel approaching in size the popliteal itself in which recent thrombosis had taken place. He also states that after obstruction of the popliteal artery, a vessel comparable with the radial in size is felt beating within the sheath of the internal popliteal nerve, if this is exposed.

The intranēural distribution, as revealed by the microscope, has been described by Ranvier(4), and consists of a perifascicular and an intrafascicular network composed of longitudinal vessels with transverse or oblique anastomoses. There is also a macroscopic arrangement of vessels revealed in this work by the taking of radiographs of injected nerves.

Adult and foetal arms were used. The adult arms were injected *via* the third part of the subclavian artery, except two, which were injected from the great vessels close to their origin from the aorta. The foetuses were injected from the thoracic aorta. The injection material was a vermilion mass elabo-

rated by F. R. Ferguson (5). As a result of the method of injection, the blood supply of the roots and trunks of the brachial plexus could only be examined in the foetal and two of the adult arms.

For the detail of the intraneural distribution, foetuses were injected with a carmine gelatin mass.

The results have been put in the form of tables which with a little explanation will speak for themselves. Numbers 1 to 8 in the tables are adult arms and 9 to 25 foetal arms. In Table I the cervical root numbers are preceded by the letter "C" and the dorsal ones by the letter "D." The vessel called the "accessory ascending cervical" artery is, as far as my information goes, a hitherto unnamed vessel which arises from the second part of the subclavian artery and is distributed to the plexus, but may give spinal branches accompanying the sixth and seventh cervical roots in series with the branch

Table I. *Brachial Plexus—Roots*

	Ascending cervical	Accessory ascending cervical	Inferior thyroid	Posterior scapular	Subclavian	Superior intercostal
7	C 5	C 6, 7	—	—	—	C 8; D 1
8	C 5, 6, 7	—	—	—	—	C 8; D 1
9	—	—	—	—	—	—
10	—	—	—	—	—	—
11	C 5, 6	—	—	C 7, 8	—	—
12	C 5, 6	—	C 7, 8; D 1	—	—	—
13	C 5, 6	—	—	—	C 7	—
14	C 5, 6	—	—	—	—	C 7, 8; D 1
15	C 5	C 6, 7	—	—	—	C 8; D 1
16	—	C 5, 6, 7	—	—	—	C 8; D 1
17	C 5, 6	—	—	—	C 7	C 8; D 1
18	C 5, 6	C 6, 7, 8	—	—	—	D 1
19	C 5	C 5, 7	—	—	—	C 8; D 1
20	C 5	—	—	C 6, 7	—	C 8; D 1
21	C 5	C 6, 7	—	—	—	C 8; D 1
22	C 5	—	—	—	—	C 6, 7, 8; D 1
23	C 5	C 7	—	C 6	—	C 8; D 1
24	C 5	C 6	—	—	—	C 8; D 1
25	—	C 7	C 5, 6	—	—	C 8; D 1

which the ascending cervical artery then gives along the fifth root. This branch occurred in 6 of my cases and a branch with the same distribution arose from the costo-cervical trunk in 4 cases, so that it may be said to have been present in 10 out of the 17 cases. As will be seen from the table C 5, 6 and 7 roots are usually supplied by the ascending and accessory ascending cervical arteries, and C 8 and D 1 roots usually by the superior intercostal artery.

In Table II the supply to the trunks of the plexus is seen to be less constant.

When Table III records that "All 3" cords were supplied by the axillary artery, it means that they were supplied by a single branch.

In Tables VIII and IX the naming of certain branches requires explanation. In Table VIII the branches of the superior profunda artery are divided into proximal, distal and indirect. In 22 cases the superior profunda divided into two almost equal vessels which accompanied the nerve on opposite sides

as far as the external intermuscular septum. These are named proximal and distal according to their positions at their origin. It is the proximal branch

Table II. *Brachial Plexus—Trunks*

	Ascending cervical	Accessory ascending cervical	Thyroid axis	Posterior scapular	Subclavian	Costo-cervical	Axillary
7	—	—	—	U, M	—	—	L
8	—	U, M, L	—	—	—	—	—
9	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—
11	—	—	—	—	—	—	U, M, L
12	—	—	—	—	—	—	U, M, L
13	—	—	U	—	M	—	L
14	—	—	U	—	M, L	—	—
15	—	U, M, L	—	—	—	—	—
16	—	U, M, L	—	—	—	—	—
17	—	—	—	—	U, M	—	—
18	—	U, M	—	L	—	—	—
19	—	U	—	—	—	—	M, L
20	—	—	—	U, M, L	—	—	—
21	—	U, M, L	—	—	—	—	—
22	—	—	—	U, M, L	M	M, L	—
23	—	—	—	—	—	—	U, M, L
24	—	—	—	—	—	M, L	—
25	—	—	—	—	—	—	—

U = Upper trunk. M = Middle trunk. L = Lower trunk.

Table III. *Brachial Plexus—Cords*

	Axillary	Brachial	Thoracic axis	Subclavian	Costo-cervical	Posterior scapular
1	All 3	—	—	—	—	—
2	,,	—	—	—	—	—
3	,,	—	—	—	—	—
4	,,	O, I	—	—	—	—
5	—	—	—	—	—	—
6	All 3	—	—	—	—	—
7	,,	—	—	—	—	—
8	,,	I	—	—	—	—
9	,,	—	—	—	—	—
10	I, P	—	O	—	—	—
11	I, P	—	O	—	—	—
12	All 3 + O	—	—	—	—	—
13	O, I, P	—	—	—	—	—
14	All 3 + I	—	—	—	—	—
15	—	I, P	O	O	—	—
16	All 3 + I, P	—	—	—	—	—
17	All 3 + O, I	—	—	O, P	—	—
18	O, I, P	—	—	—	—	—
19	O, P	I	—	—	—	—
20	O, I	—	—	—	—	P
21	O, I, P	O	O	—	—	—
22	—	—	O	I, P	—	—
23	All 3	—	—	—	—	—
24	I, P	—	O	—	P	—
25	P	—	—	O, I, P	—	—

O = Outer cord. I = Inner cord. P = Posterior cord.

which accompanies the nerve through the intermuscular septum. The indirect branches are from muscular branches which arise before the division of the main trunk. In Table IX the separation into proximal and distal branches

Table IV. *Median Nerve (Upper Arm)*

	Thoracic axis	Axillary		Brachial		Anastomotica magna	Total
		Direct	Indirect	Direct	Indirect		
1	—	—	1	4	—	—	5
2	—	—	1	3	1	—	5
3	—	1	—	2	—	—	3
4	—	—	—	2	—	1	3
5	—	—	—	4	—	1	5
6	—	1	—	1	—	1	3
7	—	—	2	—	1	1	4
8	—	—	—	3	—	—	3
9	—	1	—	2	—	—	3
10	—	—	—	1	—	1	2
11	—	—	—	1	1	1	3
12	—	—	—	1	1	1	3
13	—	—	—	2	2	—	4
14	—	1	—	4	—	—	5
15	1	—	1	2	2	1	7
16	—	—	1	2	1	1	5
17	—	1	—	2	—	—	3
18	—	—	2	1	1	—	4
19	—	—	1	—	1	1	3
20	—	1	—	3	—	—	4
21	—	1	—	—	1	—	2
22	—	1	—	2	—	1	4
23	—	1	—	1	1	1	4
24	—	—	—	2	1	—	3
25	—	1	—	1	2	1	5
Total	1	10	9	46	16	13	95

Average number of branches per case = 3·8.

Table V. *Median Nerve (Forearm)*

	Comes nervi mediani	Ulnar		Radial		Anterior ulnar recurrent	Anterior interosseous	Superficialis volae	Total
		Direct	Indirect	Direct	Indirect				
1	—	1	—	—	2	—	—	—	3
2	9	—	—	—	—	1	—	—	10
3	6	—	—	—	—	2	—	—	8
4	—	1	1	1	1	1	—	1	6
5	—	1	—	1	—	1	—	—	3
6	—	—	—	1	3	1	1	—	6
7	—	—	—	—	3	1	1	—	5
8	—	—	—	—	4	—	2	—	6
9	—	4	—	2	—	—	1	—	7
10	3	—	2	—	2	2	—	—	9
11	4	1	—	—	—	—	1	—	6
12	5	—	—	1	—	1	—	—	7
13	6	—	1	1	—	—	1	—	9
14	—	—	—	—	4	—	3	—	7
15	7	—	—	—	—	1	—	—	8
16	—	—	2	—	2	—	1	—	5
17	—	—	1	—	1	1	2	—	5
18	6	—	—	—	—	1	—	—	7
19	6	—	—	—	—	1	—	—	7
20	5	—	—	—	—	—	—	—	5
21	7	—	—	—	—	1	—	—	8
22	5	1	—	—	—	—	—	—	6
23	4	—	1	—	—	—	—	—	5
Total	73	9	8	7	22	15	13	1	148

Average number of branches per case = 6·4.

Table VI. *Ulnar Nerve (Upper Arm)*

	Axillary	Sub-scapular	Brachial		Inferior profunda	Anasto-motica magna	Superior profunda	Total
			Direct	Indirect				
1	1	—	—	—	2	2	—	5
2	1	—	—	—	2	2	1	6
3	1	—	—	—	3	1	—	5
4	1	—	—	—	1	1	1	4
5	1	—	—	—	2	1	—	4
6	1	—	—	1	3	—	—	5
7	1	—	—	—	2	1	—	4
8	1	—	—	—	2	1	—	4
9	1	—	1	—	1	—	—	3
10	1	—	1	—	4	—	—	6
11	1	—	1	1	2	—	—	5
12	—	1	—	—	3	—	—	4
13	1	—	—	—	1	—	—	2
14	1	—	—	—	1	1	—	3
15	1	—	—	—	2	1	—	4
16	1	—	—	—	2	1	—	4
17	—	—	1	—	2	—	—	3
18	1	—	—	—	2	1	—	4
19	1	—	—	—	2	—	—	3
20	1	—	—	—	1	2	—	4
21	1	—	—	—	1	—	—	2
22	—	1	—	—	1	1	1	4
23	1	—	—	—	1	—	—	2
24	1	—	—	—	1	—	—	2
25	—	—	1	—	3	—	—	4
Total	21	2	5	2	47	16	3	96

Average number of branches per case = 3·8.

Table VII. *Ulnar Nerve (Forearm)*

	Posterior ulnar recurrent	Ulnar		Total
		Direct	Indirect	
1	3	3	1	7
2	3	5	—	8
3	3	5	—	8
4	2	3	2	7
5	3	2	5	10
6	2	4	—	6
7	1	2	2	5
8	1	2	2	5
9	2	6	—	8
10	3	2	3	8
11	3	2	2	7
12	2	2	3	7
13	2	4	1	7
14	2	2	4	8
15	2	3	4	9
16	2	2	4	8
17	2	2	3	7
18	3	3	3	9
19	2	2	2	6
20	2	2	3	7
21	1	2	3	6
22	2	1	4	7
23	2	3	1	6
24	2	4	—	6
25	2	3	2	7
Total	54	71	54	179

Average number of branches per case = 7·16.

again requires explanation. While the posterior interosseous nerve is in the substance of the supinator brevis muscle, it is supplied by twigs from an anastomosis between the radial recurrent and posterior interosseous arteries. The anastomosis is composed of two main vessels which lie on opposite sides of the nerve and are named according to their position. In cases 3, 4 and 11 I have no record of the actual source of the vessels.

In the remainder of this article I shall indicate briefly the conclusions which can be drawn from the tables and mention a few points which do not occur in them.

The obvious conclusion is that the blood supply to the nerves is inconstant. The first law of Quénu and Lejars, quoted above, is contradicted. Their second law is confirmed. It is a rule that each branch divides when near the nerve and sends a branch proximally and one distally. There are a few exceptions to this rule—notably the branch of the axillary artery, which goes to the point of division of the inner cord of the brachial plexus and only extends distally.

The brachial plexus does not differ from the nerves of the arm in the nature of its supply.

There are some differences between the upper arm and the forearm in the arteries to the nerves. The average number of branches is greater in the forearm, but the branches are also smaller: it is less common to find the vessels running for any distance on the surface of the nerve in the forearm, but this may be simply a consequence of their volume; the blood supply is actually better in the upper arm than in the forearm.

The musculo-spiral nerve differs from the median and ulnar in having a larger number of branches. It is difficult to say from dissections whether the blood supply is greater, but microscopic sections of injected nerves indicate that it is so. Compton (6) suggests that the better recovery of the posterior tibial bundle of the sciatic nerve is dependent on its better blood supply. It is therefore possible that the recovery of the musculo-spiral may be affected by its blood supply, but other factors undoubtedly contribute to the good prognosis which may be given after suture of this nerve.

The vessels to the posterior interosseous nerve are exceedingly fine, and suggest that the blood supply to this nerve is poor. When sections of the posterior interosseous and radial nerves are compared, it is found that the area of nervous tissue in the two is about equal, but the area of the blood vessels in the radial is three and a half times as great as the area of the blood vessels in the posterior interosseous. The posterior interosseous has very little interfascicular connective tissue. It seems to me that the fineness of the vessels to this nerve may be the reason why the muscles supplied by it are paralysed in lead poisoning. The supinator longus muscle being supplied by the musculo-spiral would escape.

In radiographs of injected nerves a continuous chain of vessels can be seen along the whole length of the nerves, and the finer vessels anastomose

Table VIII. *Musculo-spiral Nerve*

	Axillary	Sub-scapular	Brachial		Superior profunda			Radial recurrent	Total
			Direct	Indirect	Proximal	Distal	Indirect		
1	—	1	—	1	6	3	—	—	11
2	—	1	—	—	1	1	1	—	4
3	—	1	—	—	1	1	1	—	4
4	1	—	—	—	1	2	—	—	4
5	1	—	—	1	1	3	—	—	6
6	—	1	—	1	3	3	—	1	9
7	—	—	—	1	2	1	—	1	5
8	1	—	—	1	2	—	—	1	5
9	1	—	—	1	2	2	—	—	6
10	—	—	—	—	2	1	—	2	5
11	—	1	—	2	4	—	—	—	7
12	—	2	—	1	4	—	—	2	9
13	—	1	—	—	2	—	1	1	5
14	—	—	—	—	1	3	2	2	8
15	—	—	—	2	4	1	—	1	8
16	1	—	—	1	2	1	1	1	7
17	1	—	—	—	2	2	—	1	6
18	1	—	—	—	3	1	—	3	8
19	—	1	—	1	4	—	—	—	6
20	—	1	—	1	2	2	—	—	6
21	—	—	—	—	1	2	—	1	4
22	—	1	1	—	—	3	—	—	5
23	—	1	1	—	4	—	—	1	7
24	—	1	—	1	2	—	—	1	5
25	—	—	—	2	3	1	—	—	6
Total	7	13	2	17	59	33	6	19	156

Average number of branches per case = 6·2.

Table IX

Posterior Interosseous Nerve

	Radial recurrent and post. interosseous		Radial recurrent	Total
	Proximal	Distal		
1	2	3	—	5
2	—	—	—	—
3	4		—	4
4	6		—	6
5	2	4	—	6
6	3	1	—	4
7	—	3	—	3
8	4	2	—	6
9	2	—	1	3
10	3	2	—	5
11	2		1	3
12	2	1	—	3
13	2	2	—	4
14	2	1	—	3
15	2	—	—	2
16	2	2	—	4
17	1	1	—	2
18	2	4	—	6
19	—	—	—	—
20	—	—	—	—
21	—	—	—	—
22	2	2	—	4
23	—	—	—	—
24	—	—	—	—
Total	31	28	2	73

Average number of branches per case = 4·05.

Radial Nerve

	Radial recurrent	Radial		Total
		Direct	Indirect	
1	4	—	3	7
2	2	1	1	4
3	2	1	1	4
4	2	1	1	4
5	1	1	2	4
6	1	—	4	5
7	1	—	3	4
8	2	—	2	4
9	2	—	4	6
10	—	—	4	4
11	—	2	4	6
12	2	—	5	7
13	—	4	1	5
14	1	1	1	3
15	—	2	—	2
16	1	—	4	5
17	1	—	4	5
18	2	—	4	6
19	2	—	2	4
20	—	—	—	—
21	2	1	3	6
22	2	—	2	4
23	—	—	—	—
24	2	—	1	3
Total	32	14	56	102

Average number of branches per case = 4·6

Table X. *Musculo-cutaneous Nerve*

	Axillary	Brachial		Anastomotica magna	Total
		Direct	Indirect		
1	2	—	6	—	8
2	—	—	6	—	6
3	—	1	4	—	5
4	—	—	5	—	5
5	1	—	6	—	7
6	3	—	4	—	7
7	—	—	5	—	5
8	—	—	3	—	3
9	2	—	6	—	8
10	3	—	2	—	5
11	2	—	5	—	7
12	4	—	3	—	7
13	2	—	4	—	6
14	2	—	4	—	6
15	3	—	5	—	8
16	1	—	4	—	5
17	2	—	5	1	8
18	3	—	5	—	8
19	1	—	2	—	3
20	—	—	—	—	—
21	1	—	3	—	4
22	1	—	3	—	4
Total	33	1	90	1	125

Average number of branches per case = 5·9.

freely. There is in this quite sufficient evidence to show why nerve trunks can survive after being stripped over a considerable length.

I am indebted to Professor Stopford for many suggestions and for material from the Anatomy Department at Manchester University. I obtained foetuses from St Mary's Hospital, Manchester. To Dr F. R. Ferguson I am indebted for permission to use his injection mass before his results were published.

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A CONTRIBUTION TO THE DEVELOPMENT OF THE DUODENUM

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The development of the adult digestive tract from a simple tubular structure is the result of a series of growth changes which take place in different regions of the primitive gut. These changes are at first mainly in the direction of increasing the length of the gut tube without any marked change in its diameter. Four regions are recognised where axial growth proceeds rapidly. In the first region—the oesophageal—the gut growth and the growth of the cervical and the thoracic regions of the body proceed at approximately the same rate. In the other regions, i.e. from the cardiac end of the stomach to the junction of the gut with the proctodaeum, the gut increases much more rapidly in length than the abdominal cavity, hence loops of gut are formed which have been described by Bardeen (1) as

(*a*) The gastro-duodenal.

(*b*) The entero-colic.

(*c*) The colic loops.

The first loop he describes as giving rise to the adult stomach and the upper part of the duodenum. The second gives rise to the remainder of the duodenum, all the small intestine and the large bowel as far as the middle of the transverse colon. The third loop develops into the remainder of the large intestine.

Robinson (2) recognises three factors which come into play in determining the final position of the adult gut tube:

(*a*) The growth changes in the gut itself.

(*b*) The growth of neighbouring organs.

(*c*) The method of attachment of the mesodermic mesentery and the length of this mesentery which determine the amount of free movement of the part of the gut to which it is attached.

The view of Bardeen (1) that the duodenum is developed from the adjacent ends of the first and second loops is not taken by Frazer and Robbins (3), who hold that the duodenum is not developed in this manner, but that a segment of the primitive gut tube between the ends of the first and second loops remains unchanged during the formation of the three primary loops. This segment at a later period develops into the duodenal loop.

In a subsequent paper Frazer (4) gave as his opinion that the segment between the two upper primary intestinal loops was "elongated in accordance

with and was curved out by the growth of the head of the pancreas" to form the adult duodenum.

But a consideration of the following facts shows that the growth of the head of the pancreas cannot be the sole factor producing the loop of the duodenum:

(*a*) Numerous cases are on record of adult human subjects in whom a duodenal loop is described as being present, hanging from the dorsal abdominal wall, by a mesentery, the head of the pancreas not being contained within the loop, but lying behind or to the side of the gut (Reid (5), Papez (6), Bryce (7), Eddy (8), Clermont (9)).

(*b*) Again, if Frazer's view be strictly correct, one would not expect to find a curved duodenum in animals which do not possess a part of the pancreas in the form of a distinct "head" as it is found in the human organ. In a number of animals, however, in which such a "head" is absent, the duodenum still forms a distinct loop. In an article by Carner (10), figuring a number of specimens of the injected pancreas in the developing pig, a distinct duodenal loop appears to be the normal condition, yet the pancreas of this animal bears nothing in the nature of a "head" which would cause the loop. Sisson (11) describes this pancreas as being triangular in form. In the horse the duodenum forms a distinct loop, suspended from the dorsal abdominal wall by a mesentery, but the shape and position of the pancreas are such that it cannot have caused the duodenal loop. In the ox and in the sheep, in each of which there is a large complex stomach and a relatively small though distinct duodenal loop, the pancreas is so irregular in form that it appears impossible that it should have any influence in the shaping of the gut. In the cat and in the dog the form of the duodenum strongly resembles the form in man, yet the pancreas consists of two long narrow limbs, one limb passing across the dorsal wall of the abdomen, the other limb following the curve of the intestinal wall, and lying within the folds of the mesoduodenum. It appears improbable that such a slender band could be the sole factor in producing the curve of the duodenum.

(*c*) Further, in the human embryo at a period when the duodenal loop is well developed, the pancreas is a relatively unformed structure, lying more or less diffusely in the mesentery. This is clearly demonstrated by an examination of the wax-plate reconstruction of a 22 mm. human embryo (fig. 5) and the horizontal section of the same embryo through the duodenum, dorsal mesentery and pancreas (fig. 2).

The above evidence seems to make it clear that some influence or influences other than the growth of the "head" of the pancreas must be at work to produce the curve of the duodenum, as in each case the pancreas bears a different relation to the duodenal loop.

The wax-plate reconstruction of a 6 mm. human embryo is shown in fig. 3. In it a short length of intestine is seen between the primary gastric and enterocolic loops. It is attached to the dorsal abdominal wall by a thickened part of the mesentery. The upper limit of this part of the mesentery (the mesoduodenum) is just below the opening of the bursa omentalis (the foramen of

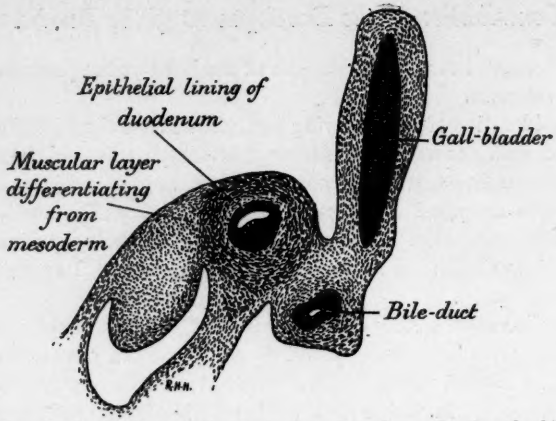

Fig. 1. H.S. through the duodenum of a 6 mm. human embryo, showing the bile duct on the postero-lateral aspect of the gut.

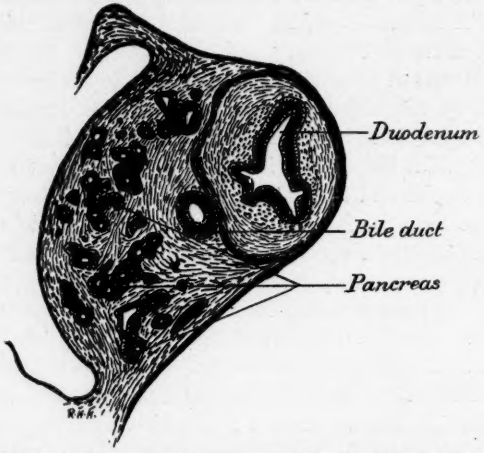

Fig. 2. H.S. through the duodenum and dorsal mesentery of a 22 mm. human embryo, showing the bile duct on the postero-medial aspect of the gut.

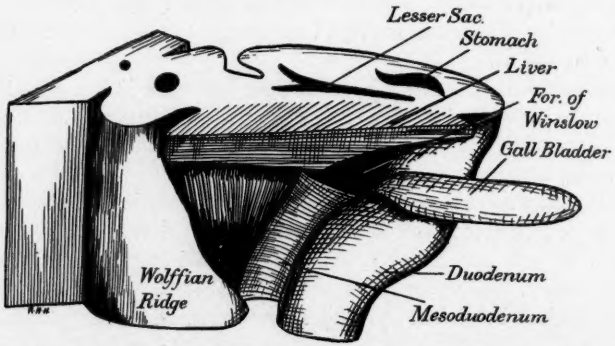

Fig. 3. Wax-plate reconstruction of the duodenal region of a 6 mm. human embryo. This reconstruction demonstrates the small segment of gut between the gastro-duodenal and the entero-colic loops of Bardeen from which is developed the major portion of the duodenal loop. The lower part of the liver has been removed, and the reconstruction viewed from the right side.

Winslow of the adult), of which it forms the lower boundary, while its lower limit is marked off from the remainder of the mesentery by a small recess, which is thus situated between the rounded lower border of the mesoduodenum and the mesentery of the entero-colic loop. It is from this short length of the gut that the second, third and fourth parts of the duodenum are developed. To demonstrate the changes in the form of the developing duodenum, wax-plate reconstructions of this part of the gut were made from 13, 22 and 30 mm. human embryos. In the 13 mm. stage the duodenal gut appears to be fixed at the upper and lower attachments of the mesoduodenum, by what may be termed "fixation bands." The upper of the "fixation bands" is beyond the pylorus. It is formed by a condensation of mesenchyme which extends from the tissue of the septum transversum round the right gastric blood-vessels to the junction of the duodenum with the pylorus. The lower "fixation band" is formed by a condensation of the mesenchyme round the superior mesenteric artery. It corresponds in position to the muscle of Treitz. Frazer and Robbins (12) are unable to discover "undoubted evidence" of the presence of this muscle before the 35 mm. stage, that is, at a period when the duodenal form is practically completed. They state, however, that the method employed in staining their preparations may make more difficult the recognition of the band before this time. In the series of embryos available in Belfast University a distinct condensation of mesenchyme can be seen around the right gastric and superior mesenteric blood-vessels in the 22 mm. stage and a condensation can even be seen in the 13 mm. stage. It is at this latter stage that the first indication of the looping of the duodenum occurs. The synchronous appearance of these two bands of tissue and the beginning of the looping of the duodenum suggest that in some way the form of the gut is influenced by, if not dependent on, their presence, that they fix the proximal and distal ends of the duodenum and prevent it taking part in the entero-colic loop.

From the pyloric end of the stomach to the upper fixation band there is a segment of small intestine which develops into the first part of the duodenum in the adult. This segment always has a distinct mesentery even in the adult. It is the terminal part of the gastro-duodenal loop of Bardeen. Hence the stages in its development are closely connected with the growth changes in the stomach and are only partly related to the development of that part of the duodenum which is attached to the posterior abdominal wall between the upper and lower fixation bands described above.

Between the 6 mm. stage and the 13 mm. stage the whole of the gut grows considerably in length and this lengthening affects the duodenum between the fixation bands in such a way as to produce looping of this portion. The growth commences from the cranial end and a loop is produced in a sagittal plane convex forwards. The lower half of the duodenal segment then commences to grow in length, but owing to the shortness of the mesoduodenum and the presence of the large mesentery of the entero-colic loop with the rapidly growing upper limb of this loop, it is forced to grow laterally to form another

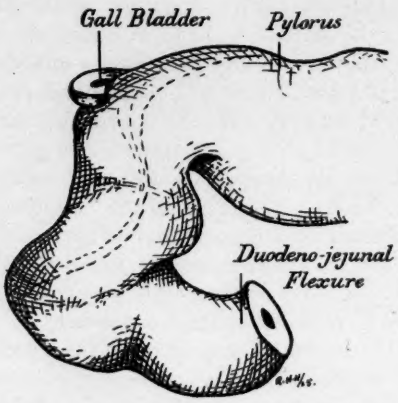

Fig. 4. Wax-plate reconstruction of the duodenum of a 13 mm. human embryo, showing the second stage in the development of the loop. The reconstruction is viewed from the ventral surface of the embryo.

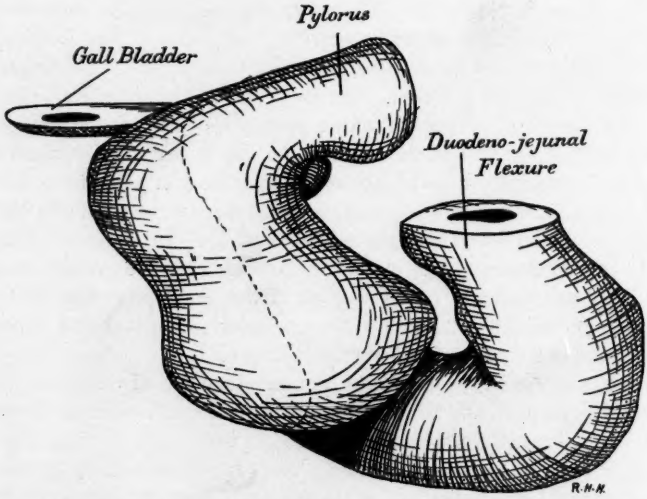

Fig. 5. Wax-plate reconstruction of the duodenum of a 22 mm. human embryo, showing the third stage in the development of the loop. The reconstruction is viewed from the ventral surface of the embryo.

distinct loop in a coronal plane and with its convexity directed caudally and to the right. In the 13 mm. stage this double looping of the duodenum is to be seen (fig. 4). With the continued rotation of the stomach to bring the original ventral or anti-mesenteric border into a horizontal plane, the upper loop of the duodenum is forced to rotate in the same direction, and hence this original ventral loop tends to be twisted to the right so that the original right side of the mesentery now lies more and more in a coronal plane and the whole loop becomes a single loop concave to the left. The rotation is well shown in the altering position of the opening of the common bile duct which changes from a dorso-lateral position to a dorso-medial position (figs. 1 and 2). In the 22 mm. embryo the upper part of the loop is seen to have rotated slightly and the whole of the duodenum is now lying to the right of the middle line. As this axial

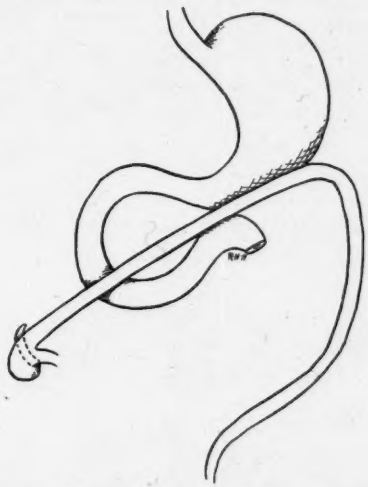

Fig. 6. Diagram of the stomach, duodenum and colon of a 44 mm. human foetus, showing the final stage in the development of the duodenal loop. (From a reconstruction.)

rotation continues the anti-mesenteric border of the duodenum lies entirely in a coronal plane and the whole of the loop is in contact with the posterior abdominal wall.

About the 40 mm. stage the extra-abdominal gut becomes included within the limits of the abdominal cavity and a further change takes place in the duodenal region. The caecum and the remainder of the large gut on their entry into the abdomen occupy a position directly under the anterior edge of the liver. Gradually, owing to the rapid growth of the small intestine and of the whole abdominal cavity and a relative shortening of the mesocolon, the large gut migrates more and more posteriorly until it occupies a position along the posterior abdominal wall. As the colon comes into contact with the duodenal

loop it completes the folding backwards of the duodenum against the dorsal wall of the abdomen, and also adheres to the duodenum at the point of crossing (fig. 6). The mesoduodenum up to this stage is complete, but soon, however, the gut takes up its adult retro-peritoneal position by the disappearance of the mesothelial cells of the parietal peritoneum and those of the dorsal or right layer of the mesoduodenum.

CONCLUSIONS

1. The duodenum, from the developmental point of view, is not simply a part of the small intestine, but is developed separately and is liable to variation without involving other parts of the intestine.

2. The duodenum owes its adult position to three factors acting on the developing gut segment:

(*a*) A series of differential growth changes which lead to the formation of two loops in the primitive straight duodenum.

(*b*) The position of these loops governed by changes which take place in neighbouring organs and which force the tube to take the form shown in the various stages.

(*c*) The disappearance of the mesentery after the colon and the duodenum have assumed their adult relations to the posterior abdominal wall. The duodenum and the colon adhere together by a fusion of their peritoneal coats at the point where they cross.

3. The pancreas, far from influencing the form of the duodenal loop, seems to grow along the planes of least resistance and to be moulded by the neighbouring organs rather than mould them.

In conclusion I wish to thank Professor Walmsley for his valuable advice in the preparation of this article.

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ON THE DISTRIBUTION OF THE ELASTIC TISSUE IN THE BLOOD VESSELS OF BIRDS

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The structure of the aorta, of its branches, and of the arteries of the limbs of birds has been described by Argaud (*Comptes Rendus de l'Association des Anatomistes*, 1904).

In this work Argaud showed that in birds the transition from the elastic to the muscular type of artery takes place in the aorta, the lower end of which belongs in some birds entirely to the muscular type.

Argaud pointed out that in the aorta of the Eagle the elastic tissue near the intima is arranged longitudinally, the fibres forming a close sheath for the muscle bundles, whereas nearer the adventitia this network becomes transversely elongated and forms complete fenestrated laminae. At a lower level the elastic tissue near the intima is completely replaced by muscle, and near the adventitia it forms a close network in which several continuous circular elastic laminae can be found.

Argaud showed also that the superior mesenteric artery differs from its branches and from other arteries in that it contains a layer of longitudinal muscle fibres in the adventitia. He also pointed out that in the Eagle the arteries of the wings possess the structure of large arteries and are elastic in type, whereas those of the legs belong to the muscular type.

In this study the arteries of the following birds were examined:

Great Tit (*Parus major*).
Blue Tit (*Parus caeruleus*).
Sparrow (*Passer domesticus*).
Starling (*Sturnus vulgaris*).
Robin (*Luscinia rubecula*).
Jack Snipe (*Gallinago gallinula*).
Moorhen (*Gallinula chloropus*).
Pigeon (*Columba livia*).

METHODS

The tissues were fixed in 10 per cent. formol, or in Mann's picro-corrosive-formol solution, and embedded in paraffin. Sections were cut 3–6 μ thick and were stained according to the following methods.

After removing the paraffin the slides were passed through absolute alcohol and covered with freshly made Weigert's elastic tissue stain. This was allowed

to act for twelve minutes, care being taken to keep the slides covered with stain. They were then washed in three changes of 95 per cent. methylated spirit to remove surplus stain. When the sections appeared pale purple they were further differentiated and counterstained by placing them in a saturated watery solution of picric acid for five minutes. They were then quickly washed, dehydrated and mounted in balsam. When finished the sections were of a greenish yellow colour, and under the microscope the elastic tissue appeared a deep black against a yellow background. This method was particularly satisfactory for photographic purposes.

To show the proportion of muscular to fibrous tissue some sections were also stained with Weigert's elastic tissue stain and counterstained with van Gieson's stain. Others were stained with haematoxylin and eosin for the identification of the tissues.

GENERAL DESCRIPTION

As the aorta and large arteries have already been described in detail by Argaud, they were examined only to ascertain whether any variation in their structure exists in different classes of birds. This study therefore mainly concerns the smaller arteries and arterioles.

In almost all the arteries of the birds examined a fenestrated internal elastic lamina is found as in mammals, but there is also a definitely fenestrated external lamina. In birds one is rarely found without the other, the two laminae being almost always present together. Where the internal lamina is absent, i.e. in the aorta and smallest arterioles, there is no external lamina either. The external lamina appears continuous in both transverse and longitudinal sections and is usually much thicker than the internal. Sometimes there are two distinct external laminae in close juxtaposition which are quite separate from one another, instead of the single one usually present, but occasionally these two may show some fine connecting threads.

In the large arterial trunks there are a series of similar continuous fenestrated laminae in the media, one to eight in number.

This lamina is easily detached and, in very thin oblique sections, is seen to consist of a delicate network of elastic fibres with fairly regular round or oval holes, the fenestrae. The fenestrae are far more numerous and larger in the intermediate and external than in the internal laminae of the same vessels.

Such a fenestrated external elastic lamina has been described only in some mammals and usually in arteries containing a considerable amount of elastic tissue both in the media and adventitia, but in birds it is found in vessels where there is no other elastic tissue besides the internal elastic lamina.

The thickness of this lamina varies a good deal in different arteries and seems partly dependent on the amount of support given to the artery by the surrounding tissues. Therefore it is most developed in the mesenteric vessels, in their branches and in the arteries of the head outside the cranium. In them

a double external lamina is often present, or there is a single continuous lamina in the middle of the media in addition to an external and an internal.

In the birds dealt with in this paper the difference in the amount of elastic tissue in the arteries of the wings and legs mentioned by Argaud does not appear to exist. Indeed the arteries of the lower limbs sometimes actually contain less elastic material than those of the same calibre elsewhere.

Again, the arteries of the kidney differ from those of the same organ in mammals in that even the largest arteries contain relatively little elastic tissue. The splenic arteries also, though muscularly thick, are, for their size, very poor in elastic tissue, possessing less than any other arteries examined. Those of the lungs, on the other hand, although possessing very thin walls in proportion to their size, contain a relatively large amount of elastic tissue and very definite internal and external elastic laminae.

DETAILED DESCRIPTION OF VARIOUS VESSELS

A general description of such a vessel is given, followed by remarks upon any special difference exhibited in individual cases.

Aorta

In all the birds examined the description of the structure of the aorta given by Argaud holds good. In the thoracic aorta there is neither internal nor external elastic lamina. In the intima the elastic tissue is arranged in closely packed longitudinally running fibres lying in white fibrous tissue. The media consists of concentrically arranged bundles of muscle fibres with festooned outlines, which fit into each other; these bundles are surrounded by elastic tissue membranes. Between these membranes there is a network of thick elastic fibres running in all directions and connecting the bundles firmly to each other. Near the tunica adventitia the muscle fibres form more and more complete circular bundles, the elastic membranes become more closely crowded together and join to form fenestrated laminae, but the elastic network between them is much less dense here. The adventitia is very thin and contains a relatively large amount of elastic tissue in the form of separate longitudinal fibres. The root of the aorta and pulmonary artery of the Jack Snipe are exceptions in that they possess what appears to be a thick but discontinuous external elastic lamina.

The large arteries at the root of the neck show a structure very similar to that of the aorta itself. The amount of elastic tissue in them is very great and particularly marked near the tunica intima, where it forms a broad, close network of branching longitudinal elastic fibres with no intervening muscle. These elastic fibres are continuous with the thick elastic network between the muscle bundles.

Common Carotid Artery

The common carotid artery still shows a great deal of elastic tissue, which is here more definitely arranged in circular laminae. The intima, instead of a network, now contains only two or three irregular rows of longitudinal elastic fibres. The media consists of about six concentrically arranged muscle bundles separated by a little white fibrous tissue and surrounded by elastic membranes which form almost complete sheaths. There is very little elastic tissue between these membranes. At the margin of the media there are a few longitudinal muscle bundles, also surrounded by elastic tissue, which lie almost in the adventitia, as there is no external elastic lamina. At other points of the periphery there are several transverse elastic fibres crowded together, without intervening muscle and separating the media from the adventitia, which is much thicker in this artery, but contains less elastic tissue than in the aorta.

In the Robin the common carotid artery possesses a media, the muscle of which is no longer divided into bundles, but occupies the whole middle coat (fig. 1). The elastic tissue is arranged in a number of concentric, continuous elastic laminae at more or less regular intervals from each other. They increase in thickness from within outwards and exhibit clear spaces, which are probably fenestrae. The innermost of these laminae may be considered as the internal, and the outermost as the external elastic lamina. The adventitia contains only a few scattered elastic fibres.

External Carotid Artery

The *external and internal carotid arteries* of the Moorhen differ from each other in structure. In both the media consists almost entirely of muscle and elastic tissue, the white fibrous tissue having disappeared.

The external carotid artery has a continuous, fenestrated internal elastic lamina and in the media only a few, thin elastic fibres, arranged both obliquely and circularly and anastomosing with each other. At the junction of the media and adventitia, however, these elastic fibres form several thick fenestrated laminae packed closely together. In one section the elastic laminae of the media of the external carotid of the Moorhen are irregularly arranged. At one point they spread through the whole media, whereas at another they are all crowded together near the external lamina, so that the media here contains no elastic tissue, except at its outer edge. The adventitia is now fully one-third the thickness of the media and contains a few longitudinal elastic fibres scattered through it.

Internal Carotid Artery

The internal carotid artery has a much thinner internal elastic lamina, almost no elastic tissue in the media, but a broad layer of elastic fibres between media and adventitia. This layer consists of a continuous external elastic lamina with a large number of longitudinal elastic fibres scattered external to it.

Apart from these fibres the adventitia contains no elastic tissue although it is as thick as the media.

The internal carotid artery of the Great Tit, on the other hand, shows, as ite nters the skull, four continuous elastic laminae, an internal, an external, and two in the media. They are all of about the same thickness. As shown by a diagonal section through the artery, the membranes consist of an exceedingly fine network of elastic fibres with, from time to time, small round, oval or irregular fenestrae. These holes are largest and most numerous in the external lamina (fig. 2). The laminae are connected with each other by a loose, very irregular network of small elastic granules.

Arteries of the Trunk

In some large arteries, such as the artery which supplies the pectoral muscle of the Sparrow and one of the large abdominal arteries in the Great Tit, the elastic tissue is arranged in much the same manner as in the common carotid of the Robin. Continuous circular elastic laminae (most numerous in the vessel to the pectorals) are situated at regular intervals in the media. Although thick, these laminae are not connected by a network of elastic fibres as in the larger arteries. The external elastic lamina is replaced by a thick irregular network of fine elastic fibres lying between the media and adventitia. The latter contains a few longitudinal elastic fibres.

In the smaller arteries there is a gradual disappearance of the elastic laminae from the media, leaving only the internal and external laminae. The last indication of this change is seen in some of the medium-sized vessels of the head and abdomen where there is only one elastic lamina situated in the middle of the media, but the internal and external laminae are relatively thick. Vessels of this type have only been found in the head of the Blue Tit and the intestinal tract of the Great Tit (fig. 3).

This lamina in the media is of the same thickness as the other two, but when traced along the artery it becomes thinner, then breaks up into segments and finally into longitudinally running fibres arranged in a row about the middle of the media.

The external elastic lamina in these vessels is still reinforced by a row of longitudinal elastic fibres running parallel and immediately outside it in the adventitia.

In a few arteries of about the same size the elastic tissue of the media is no longer arranged in one plane, but consists of short membranes passing in all directions and joining with one another to form a large network which connects the internal to the external elastic lamina. In these arteries the adventitia contains relatively far more elastic tissue than in the large arteries. The best example of this structure is found in the vertebral artery of the Starling and Blue Tit just before it enters the bony canal.

Of the intestinal arteries, those with a diameter between 0·04 and 0·09 mm. possess a thick fenestrated internal elastic lamina, irregular lines of fine

elastic granules arranged in a roughly concentric manner throughout the relatively thick media, and a very thick external elastic lamina which is often double in these vessels (fig. 4), or has a thick elastic network just external to it, the fibres of which appear sometimes to spring from the external lamina.

There is also a double external lamina in some of the larger vessels of the head.

In all these vessels the adventitia is rich in elastic tissue. In no vessel examined so far has a double internal elastic lamina been found, and a double external lamina exists only in the vessels of the regions mentioned above.

Arteries of the Limbs

In the limb vessels the elastic tissue is not so abundant, the laminae are thinner and the media contains at most only a few thin elastic membranes, close to the external lamina, which in one case shows very large fenestrae (fore limb of Great Tit). The adventitia also contains a relatively small amount of elastic tissue.

The vessels of the fore and hind limbs of the Starling, Great Tit, Blue Tit, Robin and Pigeon do not show the difference in structure described by Argaud, who states that there is a greater amount of elastic tissue in the arteries of the wings than in those of the legs.

Arteries of the Lungs

The larger blood vessels of the lungs resemble somewhat the medium-sized arteries in structure although we find two distinct differences. Firstly, in proportion to their size the vessels have thin walls, the media being particularly thin. Secondly, the vessels, as in other animals, contain a relatively large amount of elastic tissue, the internal lamina being often as thick as, and sometimes thicker than the external. The media contains a fairly large number of elastic fibres arranged in irregular transverse lines. The adventitia, although thick, contains no elastic tissue except a row of longitudinal fibres parallel to the external lamina as in other large vessels.

The vessels vary in the lungs of different birds; those of the Pigeon, Great Tit, Blue Tit, and Starling are alike and their structure corresponds to the above description. In the smaller vessels there is an increase in the muscular tissue, but in the smallest the elastic tissue is present in greater proportion.

Those of the Jack Snipe and Sparrow have very thick and definite elastic coats which are continued even into the very small vessels. In the Moorhen the internal lamina and the media become relatively thicker as the artery becomes smaller; the external lamina, on the other hand, becomes thinner. As a whole, these blood vessels of the lungs contain a large proportion of elastic tissue, even in very small vessels.

Arteries of the Abdominal Viscera

The arterioles of the spleen, pancreas and kidney are peculiar in that they very rarely possess a continuous external elastic lamina, its place being taken, in the medium-sized arteries, by a thick network of elastic fibres, and in the smallest by a row of very fine longitudinal elastic fibres.

The larger arteries of the liver have a thick internal and sometimes even a double external lamina, but the arterioles have much the same structure as those of the spleen and kidney.

Arteries of the Head

The cerebral vessels have relatively much thinner walls and contain very little elastic tissue. The external elastic lamina is absent in vessels 0·08 mm. in diameter, but a trace of one is still present in a vessel of 0·124 mm. The internal elastic lamina is thin, but is present in even very small vessels (0·038 mm.). The media of all these vessels, although thin, contains a few elastic fibres.

Vessels in bony canals, such as the vertebral, have very thin walls in proportion to their diameter (fig. 5). The vertebral of the Blue Tit has a media measuring 0·007 mm., whereas its diameter is 0·195 mm. (compare this with an ordinary vessel, e.g. of diameter 0·12 mm., in which the media measures 0·033 mm.). Neither the internal nor the external elastic lamina is continuous in this vessel, but is replaced by a single row of fine elastic fibres. The media contains only a few longitudinal elastic fibres.

Arterioles

In the arterioles of the birds examined the media is entirely muscular, but there is still a distinct continuous internal and external elastic lamina, even in vessels 0·027 mm. in diameter. The persistence of this external elastic lamina is the chief characteristic of the arteries of these birds, being present in vessels which, but for the internal lamina, are entirely devoid of elastic tissue (fig. 6).

It is interesting to note that this distribution of the elastic tissue is still found in vessels of much smaller calibre in the head and intestinal tract than in other organs (e.g. head of Blue Tit 0·024 mm.—head of Great Tit 0·027 mm. —large intestine Blue Tit 0·035 mm.).

In other organs the external and sometimes the internal laminae are already discontinuous in vessels of much larger diameter (e.g. liver 0·05 mm.— ovary 0·062 mm.—lung 0·05 mm.).

As the arterioles diminish in size the external elastic lamina is the first to disappear. It breaks up into a series of longitudinal elastic fibres, which in transverse sections appear as a row of small elastic granules at the outer edge of the media. At the same time, the adventitia ceases to contain elastic fibres.

SUMMARY

1. The arteries of the birds examined possess a definite external elastic lamina which is fenestrated and often thicker than the internal lamina. It appears first in the medium-sized vessels, being absent from the branches of the aorta. This external lamina is found even in very small arterioles, the smallest being the extra-cranial arteries of the head and those of the alimentary tract. It disappears in the smallest arterioles almost at the same time as the internal elastic lamina.

2. The elastic tissue in the adventitia is present in proportion to the thickness of the external lamina; being largest in amount where the latter is thickest and disappearing completely when this breaks up.

3. Although the external elastic lamina is sometimes double, the internal lamina has never been found to be so, although in structure both laminae are identical.

4. A third elastic lamina is sometimes present in the middle of the media, as in the vessels of the head and intestine.

5. The arteries of the hind and fore limbs of these birds are identical in structure and do not possess more elastic tissue than those of the rest of the body.

I wish to express my gratitude to Professor E. Wace Carlier for his kind help and advice throughout the work.

APPENDIX

Diameter of vessels containing *elastic tissue in media*, besides an internal and external elastic lamina:

(All measurements are taken from the outer edge of the external elastic lamina.)

Blue Tit	Large intestine	0·077 mm.
	Lower limb	0·049
	Head	0·096
Great Tit	Fore limb	0·126
	Stomach	0·042
	Pyloro-duodenal junction	0·092
	Large intestine	0·044
	Lung	0·109
Moorhen	Oesophagus	0·241
	Intestine	0·039
	Mesenteric vessel	0·06
	Coronary (branch)	0·031
Jack Snipe	Lung	0·102
	,,	0·059
	Intestine	0·097
	,,	0·069
Starling	,,	0·044
Sparrow	,,	0·067
	,,	0·046
Robin	Vessel in neck	0·044
	Limb	0·082
Pigeon	Lung	0·037

Diameter of vessels with continuous external and internal lamina, but *no elastic tissue in the media*:

Blue Tit	Large intestine	0·035 mm.
	Liver	0·05
	Head (extra-cranial)	0·024
Great Tit	Oesophagus	0·048
	Stomach	0·047
	Lung	0·05
	Ovary	0·062
	Head (extra-cranial)	0·027
Moorhen	Intestine	0·09
	Lung	0·104
	Muscle of leg	0·156
Jack Snipe	Lung	0·102
	,,	0·059
	,,	0·031
Starling	Limbs	0·045
	Liver	0·044
	Intestine	0·044
Sparrow	Heart	0·032
	Lung	0·033
	Brain	0·042
	Intestine	0·075
Robin	Tongue	0·035
	Limb	0·048
Pigeon	Lung	0·056
	Intestine	0·056

Diameter of vessels in which either one or both elastic coats is *discontinuous* and in which there is no other elastic tissue:

Blue Tit	Lower limb	0·047 mm.
	,, ,,	0·021
	Head (extra-cranial)	0·032
	,, ,,	0·015
Great Tit	Large intestine	0·026
	Lymph gland	0·062
	Kidney	0·058
Moorhen	Intestine	0·039
	,,	0·09
	Pancreas	0·086
	,,	0·03
	Intestine	0·035
	Spleen	0·067
	,,	0·047
	,,	0·022
	Liver	0·031
	,,	0·081
	Kidney	0·09
	,,	0·044
	Lung	0·059
	Neck	0·025
	Thoracic wall	0·024
	Branch of coronary	0·031
Jack Snipe	,, ,,	0·166
	Lung	0·031
Starling	Heart	0·044
	Limb	0·014
	Kidney	0·11
	Intestine	0·025
Sparrow	Heart	0·032
	Brain	0·03
	Intestine	0·18
Robin	Neck vessel	0·017
	Limb	0·048
Pigeon	Lung	0·037
	Intestine	0·026
	Pancreas	0·038

EXPLANATION OF PLATE

Fig. 1. T.S. of common carotid artery of Robin. Showing the elastic tissue of the media arranged in concentric more or less complete tubular laminae.

Fig. 2. Oblique section of the internal carotid artery of the Great Tit. Showing the structure of the internal and external elastic laminae and several fenestrae in the latter. The whole vessel measures 0·19 mm. in diameter, the media being 0·03 mm. in thickness.

Fig. 3. T.S. of extra-cranial vessel in the head of the Blue Tit. Showing one complete elastic lamina in the centre of the media about midway between the internal and external elastic laminae. Diameter of vessel 0·167 mm. Thickness of media 0·03 mm.

Fig. 4. T.S. of duodenal vessel of Blue Tit. The external elastic lamina is double. Diameter of vessel 0·087 mm. Thickness of media 0·029 mm.

Fig. 5. T.S. of vertebral artery of Blue Tit lying within the vertebral canal. The wall is very thin and the external elastic lamina well marked. Diameter of vessel 0·106 mm. Thickness of media 0·015 mm.

Fig. 6. T.S. of arteries in salivary gland of Blue Tit. Showing both internal and external laminae and a media free from elastic tissue. Diameter 0·034 mm. Thickness of media 0·012 mm.

Fig. 2.

Fig. 6.

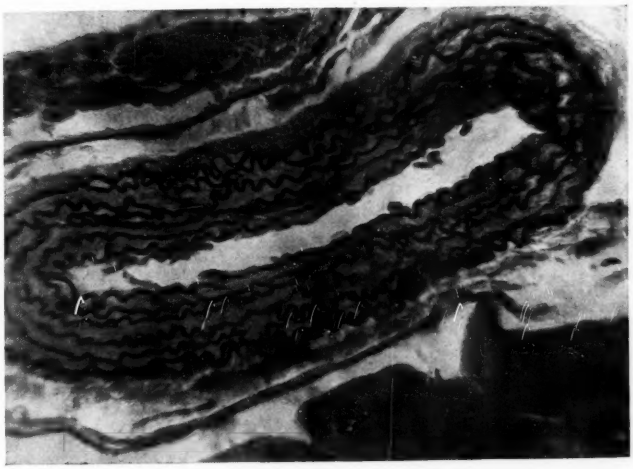

Fig. 1.

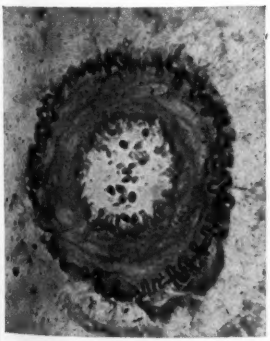

Fig. 4.

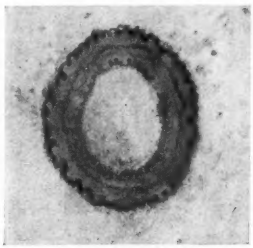

Fig. 3.

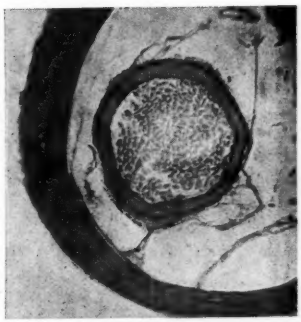

Fig. 5.

THE POSITION OF THE ABDOMINAL VISCERA IN HEALTHY, YOUNG BRITISH AND AMERICAN ADULTS

By ROBERT ORTON MOODY

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Enteroptosis, visceroptosis, gastroptosis and coloptosis have been much discussed in the medical literature of the last twenty-five years, but there is still much difference of opinion as to what these terms signify and whether or not they should be applied to normal as well as to abnormal or pathological positions of the viscera.

Some physicians make a diagnosis of gastroptosis when the lowest part of the greater curvature of the stomach is below the umbilicus, some call the stomach normal in position until the lowest part of the greater curvature is several inches below the umbilicus and some consider the position of the lowest part of the greater curvature of little significance, but make a diagnosis of gastroptosis when the lowest part of the lesser curvature is below the umbilicus. Yet another group do not make a diagnosis of gastroptosis until the lowest part of the lesser curvature is more than 2 inches below the umbilicus.

To determine the range of the normal position of the abdominal viscera and to establish a basis for a definite and accurate concept of what may rightly be called ptosis, an investigation begun at the University of California has been continued in the Department of Anatomy of University College. Radiographs have been taken of one thousand students at the University of California, an equal number of men and women, and of one hundred men and fifty women at University College, not one of whom has a history of chronic gastric or intestinal trouble.

Such a group of students is excellent material for an investigation of normal conditions for two reasons: first, because students are a healthy group with good bodily development; second, most types of healthy men and women are well represented in this group of young people. The sedentary type, the athletic type, those who work hard at manual labour during the long summer vacation, those who idly amuse themselves, those who spend much time in outdoor sport, the sthenic and the hyposthenic, with a few of the hypersthenic and asthenic, all are there. They give a fair cross-section of the physical types of healthy people that are found in most communities.

Of this group of 1150 students, at least 300 are athletes or devoting themselves specially to physical education. The development of the general musculature and of the abdominal muscles of this 300 is considerably above the average, but the position of their stomachs is like that of the rest of the group, low in some and high in others.

The weight of the barium meal given to the British students is one pound and a half, that given to the American students is somewhat more. The radiographs are taken with the subject in the anatomical position, erect.

The interiliac line, drawn between the highest points of the iliac crests, is used as a level from which to measure the position of the viscera. The iliac crests do not present a constant relation to the vertebral column, but they are easily seen in the radiographs and their relation to the vertebral column is probably more constant than that of the umbilicus, which has commonly been used as such a level.

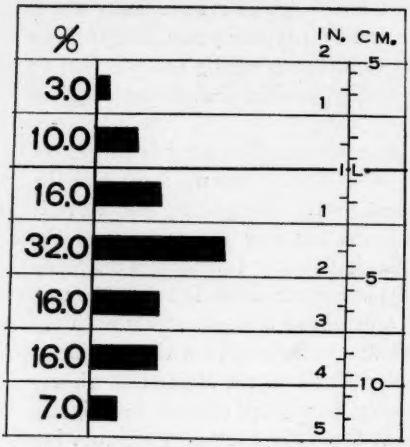

Fig. 1. Level of occurrence of the lowest part of the greater curvature of the stomach in healthy, young, British male adults.

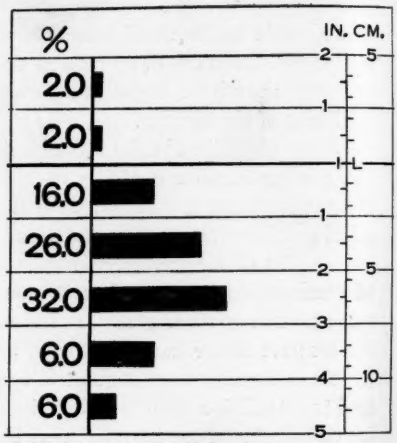

Fig. 2. Level of occurrence of the lowest part of the greater curvature of the stomach in healthy, young, British female adults.

In the graphs, the space above and below the interiliac line is divided into zones each 1 inch wide. The figures in each zone give in percentages the frequency of occurrence of the lowest part of the viscus in that zone. Zones above the line are called upper zones, those below the line are called lower zones.

In 87 per cent. of the British men, the lowest part of the greater curvature of the stomach is below the interiliac line (fig. 1). Its most frequent position is in lower zone 2, from 1 to 2 inches below the line. It is found here in 32 per cent. of the men. In 39 per cent. it is more than 2 inches below the line and in 23 per cent. it is more than 3 inches below the line.

In 96 per cent. of the British women, the lowest part of the greater curvature of the stomach is below the interiliac line (fig. 2). Its most frequent position is in lower zone 3, between 2 and 3 inches below the line. It is found here in 32 per cent. of the women. In 54 per cent. it is more than 2 inches below the line and in 22 per cent. it is more than 3 inches below the line.

This confirms what was stated as a probability in an earlier publication:

the stomachs of British men and women are lower than the stomachs of American men and women.

The background of the graph in fig. 3 is a radiograph of a male, showing the bones of the lumbar and the pelvic regions. The interiliac line in this male passes through the lower border of the fourth lumbar vertebra. Lower zone 2, in relation to the vertebral column, is in front of the lower part of the body of the fifth lumbar vertebra, the upper part of the body of the first sacral vertebra and the intervertebral disc between them. This graph shows that the lowest

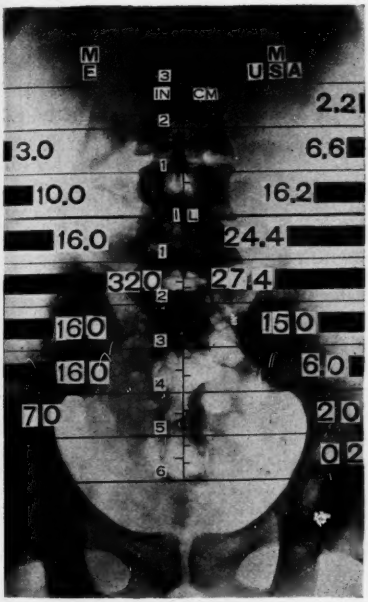

Fig. 3. Comparison of the position of the lowest part of the greater curvature of the stomach in British and American healthy, young male adults. British on left, American on right.

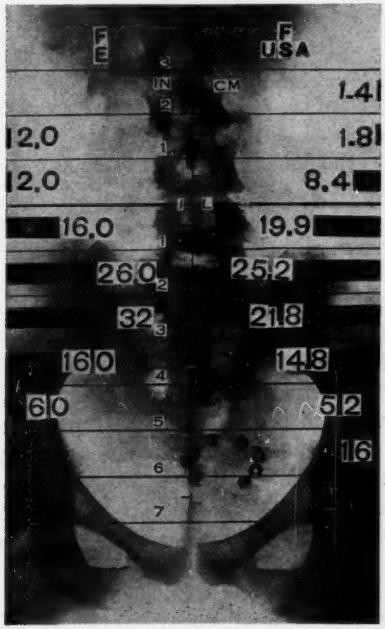

Fig. 4. Comparison of the position of the lowest part of the greater curvature of the stomach in British and American healthy, young female adults. British on left, American on right.

part of the greater curvature of the stomach is below the interiliac line in 87 per cent. of the British males and in 75 per cent. of the American males, that its most frequent position in both British and American males is in lower zone 2, but that it is found here in 32 per cent. of the British males and in 27 per cent. of the American males. In the former it is found more than 2 inches below the line in 39 per cent. and more than 3 inches below the line in 23 per cent., while in the latter it is found more than 2 inches below the line in 23 per cent. and more than 3 inches in only 8·2 per cent.

The background of the graph in fig. 4 is a radiograph of a female in whom

the interiliac line passes through the lower part of the intervertebral disc between the fourth and fifth lumbar vertebrae. This graph shows that the lowest part of the greater curvature of the stomach is below the interiliac line in 96 per cent. of British women and in 88 per cent. of American women, that in the former it is found most often in lower zone 3, between 2 and 3 inches below the line and in the latter it is found most often in lower zone 2, between 1 and 2 inches below the line. In British women it is more than 2 inches below the line in 54 per cent. and more than 3 inches in 22 per cent., while in American women it is more than 2 inches below the line in 42 per cent. and more than 3 inches in 21·6 per cent.

The lowest part of the lesser curvature of the stomach, like the lowest part of the greater curvature, is lower in both sexes in the British. The lowest part of the lesser curvature of the stomach is below the interiliac line in 34 per cent. of the British males and in only 12 per cent. of the American males. In the females, it is below the line in 42 per cent. of the British and in 30 per cent. of the Americans.

Radiographs were taken of forty-four British boys between the ages of seven and fourteen years. The barium meal given to them weighed the same as that given to the adults. The results shown in fig. 5 on the left of the graph indicate that the stomachs of the boys are higher than those of the men. The lowest part of the greater curvature of the stomach is below the interiliac line in 84·2 per cent. of the boys and in 86 per cent. of the British men and more than 2 inches below the line in 30 per cent. of the boys and in 49 per cent. of the men.

The position of the practically empty stomach in the British students was recorded by placing the lower border of a penny on the body of the subject at the level of the lowest part of the greater curvature of the stomach, after only one swallow of the barium mixture had been taken. The shadow of the penny on the radiograph not only gives a permanent record of the position of the practically empty stomach, but it also makes it easy to measure the distance that the lowest part of the greater curvature of the stomach moves downward on account of the weight of the barium meal.

The graph in fig. 6 shows that the lowest part of the greater curvature of the empty stomach is found below the interiliac line in 50 per cent. of the men and in 70 per cent. of the women. In the boys, it is below the line in 52·3 per cent. (fig. 5). It is more than 2 inches below the line in 14 per cent. of the men, in 10 per cent. of the women and in 6·8 per cent. of the boys.

The distance that the lowest part of the greater curvature of the stomach is moved down by the barium meal varies from a small fraction of an inch to 4 inches. It is most frequently moved down between 1 and 2 inches, this being the case in 58 per cent. of the men and in 47 per cent. of the women. It is moved down an inch or less in 11 per cent. of the men and in 21 per cent. of the women and between 3 and 4 inches in 3·7 per cent. of the men and in 8·5 per cent. of the women.

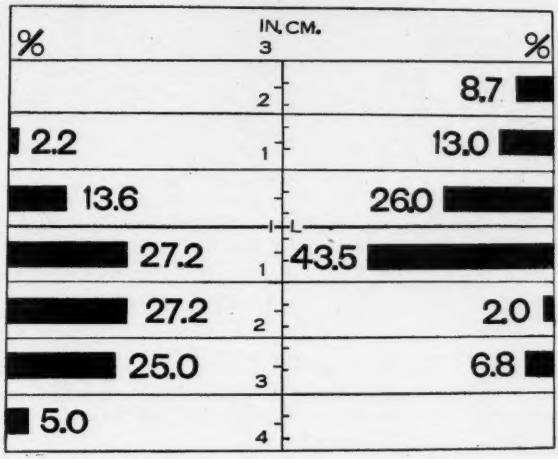

Fig. 5. Level of occurrence of the lowest part of the greater curvature of the stomach in British boys, five to fourteen years of age. After barium meal on left, empty on right.

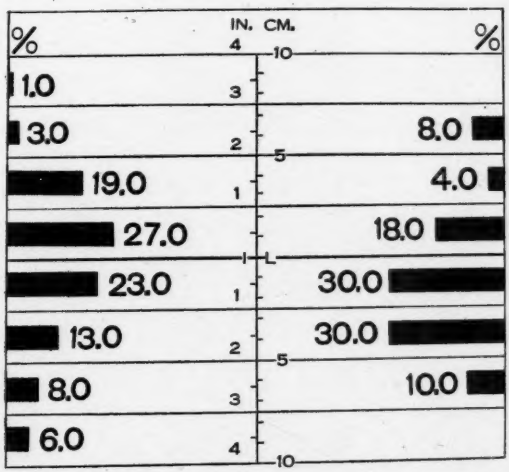

Fig. 6. Level of occurrence of the lowest part of the greater curvature of the empty stomach. British males on left, British females on right.

The figures in graphs 3 and 4 not only demonstrate that the stomachs of the British are lower than the stomachs of Americans, but they also prove that the stomachs of the British are found much more often in lower zones 3 and 4 than are those of the Americans. The lowest part of the greater curvature of the stomach is found more than 2 inches below the interiliac line in 44 per cent. of all the British students and in only 22·5 per cent. of all the American students.

That there is this marked difference in the position of the stomachs of the British and the Americans is not due primarily to any factor acting directly and specifically on the stomach. It is due fundamentally to a difference in the form of the body cavity.

The general relationship of the bodily habitus to the position of the stomach was first pointed out by Obrastow, as a result of observations made by percussion and auscultation. Mills, using radiography, confirmed Obrastow's conclusions and thought he found a much more definite and exact relation between bodily habitus and the position of the stomach. He describes two dominant types of bodily habitus, the hypersthenic and the asthenic. The hypersthenic type is characterised by a large frame, well-developed musculature, a broad, short thoracic cavity, a large intercostal angle, a broad, long abdominal cavity and a very high stomach. The asthenic type is characterised by a light frame, weak musculature, a narrow, long thoracic cavity, a narrow intercostal angle, a narrow short abdominal cavity, and a very low stomach. Between these extremes he describes a series of types and sub-types, each having a definite relation of bodily habitus to the position of the stomach.

Faber's study of healthy Scandinavian adults confirmed Mills, so far as the extreme types are concerned. He found a general relationship between bodily habitus and the position of the stomach, but no such regular and definite series between the extremes.

The present study of a much larger number of healthy, young adults confirms Faber's findings. The hypersthenic type, with the broad, short thoracic cavity, large intercostal angle and broad long abdominal cavity has, as a rule, a high stomach. As the thoracic cavity gets narrower and longer, the intercostal angle narrower and the abdominal cavity narrower and shorter, the stomach tends to be lower.

Although this relation does not vary uniformly or in a direct ratio, it is definite enough to warrant the conclusion that the stomachs of healthy young British men and women are lower than the stomachs of healthy young American men and women because the British have narrower, longer thoracic cavities and narrower, shorter abdominal cavities.

Hrdlička (1925) gives evidence that supports this conclusion. Comparing the thoracic, lateral diameters of various nationalities, he states that the thoracic lateral diameter of the thorax of the British is narrower than that of the Americans.

The position of the caecum, like that of the stomach, varies with the position of the individual. With the subject in the anatomical position the

lower end of the caecum is not often found in the iliac fossa. Its most frequent position in the British students is in the true pelvis, between 1 and 2 inches below the iliac fossa, where it is found in 45·6 per cent. of these students. It is found in the iliac fossa in only 9 per cent. (fig. 7). When the subject assumes a horizontal position the caecum moves toward the diaphragm and the lower end of the caecum is more often found in the iliac fossa.

With the subject in the anatomical position, the colon has many forms and positions. The lowest part of the transverse colon is most often found in lower

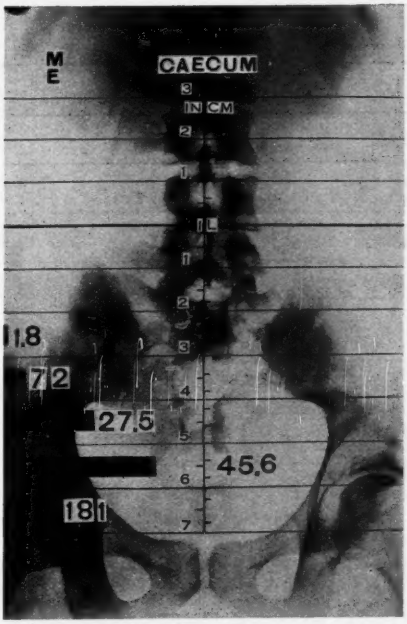

Fig. 7. Level of occurrence of the blind end of the caecum in healthy, young British adults.

zone 4, between 3 and 4 inches below the interiliac line in males and in lower zone 5, between 4 and 5 inches below the line in females (fig. 8). It is more than 4 inches below the line in 32·9 per cent. of the males and in 49·3 per cent. in the females. The hepatic flexure, the splenic flexure and the transverse colon move toward the diaphragm when the subject becomes horizontal.

The form of the liver shown in the His model and in the illustrations of most text-books is not its most common form. The lower surface of the liver, shown in the His model as lying in an almost horizontal plane is most often an inclined plane, sometimes almost parallel to the dorsal surface. The lower edge of the liver is found below the interiliac line in 52 per cent. of the men and in 42 per cent. of the women.

It has been suggested by clinicians that it is the people with low stomachs who more often have some form of gastro-intestinal trouble in middle life and old age. Since low stomachs are found in so large a number of young people it would not be strange if, among the elderly people who have gastro-intestinal trouble, many have low stomachs.

Through the courtesy of Dr Salmond of University College Hospital it has been found possible to determine the number of low stomachs in one hundred patients, an equal number of men and women, who had been radiographed because they had symptoms of gastro-intestinal trouble. The age of

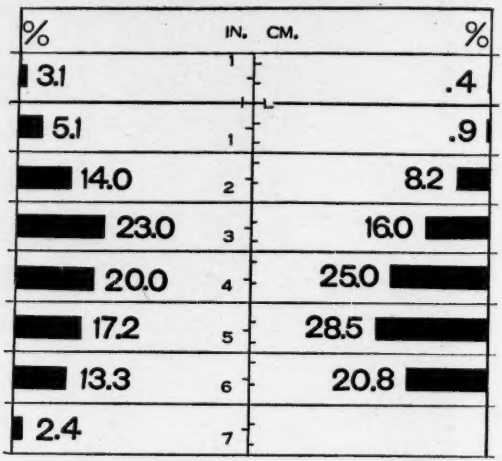

Fig. 8. Level of the lowest part of the transverse colon in healthy, young American adults. Males on right, females on left.

these patients ranged from forty to eighty-one years. The lowest part of the greater curvature of the stomach is below the interiliac line in 82 per cent. of the males and in 88 per cent. of the females. This means that low stomachs occur more frequently in the healthy young British adults than in the elderly British patients who have symptoms of gastro-intestinal trouble.

I must express my gratitude to Mr F. Melville, Radiologist in the Anatomy Department at University College, without whose technical skill the investigation in London would have been impossible.

SUMMARY

Long stomachs with the lowest part of the greater curvature as far as 6 inches below the interiliac line, the lowest part of the lesser curvature as far as 3 inches below the line and the pylorus as far as 2 inches below the line, are normal.

Transverse colons dipping far into the true pelvis are normal.

Caeca with the blind end low in the true pelvis are normal.

Livers with the lower border an inch or more below the interiliac line are normal.

The ability of the stomach, the colon and the caecum to function normally is independent of their position.

These facts justify the conclusion that enteroptosis, gastroptosis and coloptosis seldom or never exist as pathological conditions.

The use of the qualifying phrase at the end of the last paragraph would not be necessary if the terms enteroptosis, gastroptosis and coloptosis were always used with their original and proper meaning. The ending ptosis means fallen, and terms with this ending were coined and used to designate viscera that had fallen from a normal to a pathological position. The ending has not changed its meaning or significance. Therefore words with this ending should not be used to designate organs that are in normal position.

THE INTERNAL GENITAL ORGANS OF A FEMALE FOETUS OF 15 CM. LENGTH

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In order to reach a true understanding of the various malformations of the genital tract, it is important to accumulate descriptions of specimens which appear to be normal. Such an investigation has been made upon the internal genital organs of a female foetus of about 4 months' development, and the results are set forth in the following paper.

When this foetus was obtained, I was making a study of the peripheral innervation of the uterus in certain mammals. This led me to think that a description of the distribution of the nerve-tissue in this specimen might be of value. The specimen was obtained from a patient who died somewhat suddenly from Hyperemesis Gravidarum. The autopsy was carried out less than 12 hours after death. The contents of the pelvis were removed intact. The uterus was then opened, and the foetus extracted. The foetus looked quite fresh, no signs of maceration being evident. From vertex to breech it measured 15 cm. The pelvic bones and lower part of the vertebral column were dissected out carefully, and without damage to the contents of the foetal pelvis. The peritoneal cavity was then opened from in front, and the foetus divided across a short distance proximal to the internal genital organs. Unnecessary portions of the anterior abdominal wall and of the muscles of the back were then removed, leaving as complete a block as possible of the organs within the lower abdomen and pelvis. This block was fixed in Kaiserling's formalin solution, and a complete series of 2872 paraffin sections each 10 microns thick was prepared. These are numbered from the cranial extremity backwards. While the unsectioned block was in xylol, the vessels and other structures showed up so beautifully that a freehand drawing was made of the upper part of the specimen at this stage (fig. 1). The block includes the rectum posteriorly, the bladder anteriorly (portions only of the ureter being distinct on either side), and between these the genital organs. The ovaries are shaped like bay leaves, lying with their long axes horizontal. They lie proximal to and immediately above the Fallopian tubes. They extend from just within the upturned lateral end of the tube to a short distance medial to the opening of the tube into that portion of the uterus which will form the future body. The anterior surface, as indicated in the drawing, is not smooth, but shows a horizontal groove, from which side branches run as shallow sulci towards the proximal and distal borders. The tube on either side passes out from the uterus to

terminate in a curve around the lateral extremity of the ovary. In its course it is thrown into small rounded curves encountered in all planes. Relative to its length, the duct is narrower than is the adult Fallopian tube. Other details will be described later.

The drawing shows that the utero-vaginal tube consists of a long cylindrical portion a little narrower than the rectum surmounted by a short broader part which widens out proximally, and which laterally is continued into the tubes. On the cranial extremity of the upper portion a shallow medial sulcus is seen, but no evidence of the presence of a sulcus is found on the anterior surface. There is no indication on the external surface whether the line of demarcation between the distal narrow and the proximal wide portion corresponds to the dividing line between the future body and the cervix, or between the cervix and the vagina.

The blood vessels show up particularly well. On the right-hand side, the loose tissue in which they lie had been slightly damaged during the manipulations of the block, and as a result the proximal portions of the vessels were displaced outwards. For this reason, their course is not shown in the drawing. With the exception of a few reserved for special staining methods, the sections were stained with haematoxylin and eosin. Microscopically the preservation is good.

A flat reconstruction of the genital tract (fig. 2) shows its outline, the lumen being indicated by a dotted line. Remnants of Gärtner's ducts, in those parts of their course near to the utero-vaginal canal and to the tubal portion of the uterus, are seen. The tubes are long and narrow, and show the multiple curves already mentioned, but naturally only those apparent in one plane. The free end of the tube has a fimbriated extremity. Its opening faces posteriorly. From the margins of the opening strands of connective tissue are continued laterally in the edge of the mesosalpinx and also towards the ovary. At the other end, the tubes enlarge to form the tubal portion of the body of the uterus. In the reconstruction, the sulcus or the cranial extremity of the uterus at this stage of development is 0·4 mm. deep.

There is no median septum in the cavity. The formation of a single roughly symmetrical uterine cavity has kept pace with the union of the tubes to form the tubal portion of the body of the uterus. The unpaired portion of the generative tract is at this stage divisible into three portions. (1) The most proximal part is somewhat triangular in form, its base forming the future fundus of the uterus. (2) A cylindrical portion with thicker walls and a narrower cavity. (3) A long portion narrower in its proximal than in its distal half and possessing a relatively thin wall. The opening of this portion into the urogenital sinus is still closed by a solid mass of tissue. No sharp line of demarcation is present between these three portions. In length their cavities measure approximately 1·4 mm., 2·8 mm., and 5·6 mm. respectively. Diagrams illustrating the contour of a section from each of these three portions are seen in

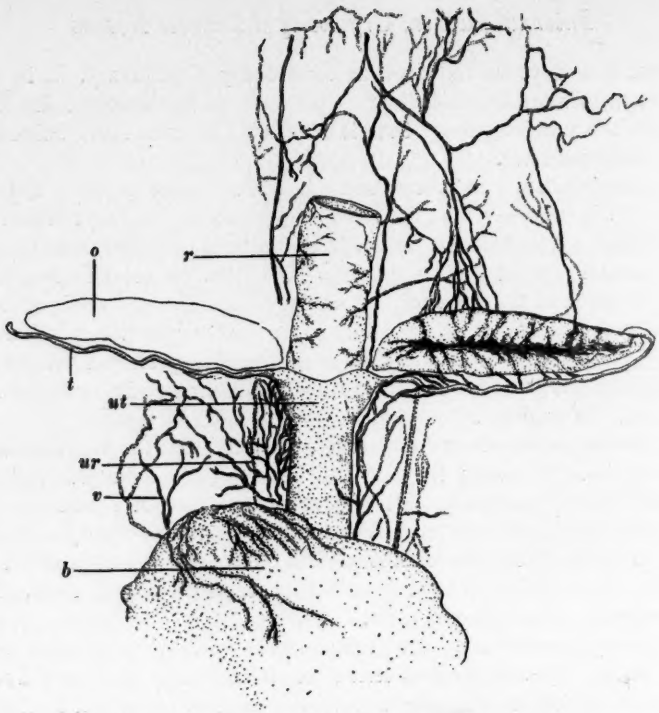

Fig. 1. Drawing of upper part of block while in xylol. b=bladder, o=ovary, r=rectum, t=Fallopian tube, ur=ureter, ut=uterus, v=blood vessels.

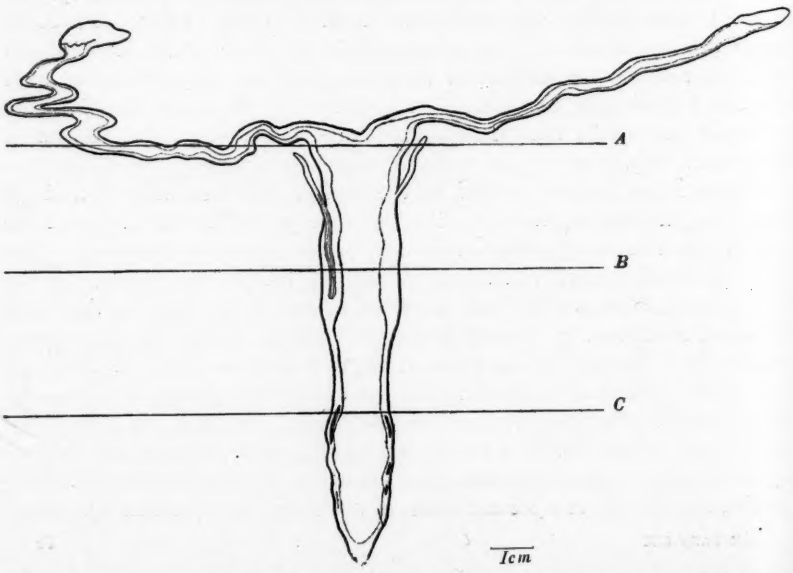

Fig. 2. Flat reconstructions of the genital tract from the serial section: for description see text. The levels from which Fig. 3 (A, B, C) are taken are indicated.

fig. 3. The region of the transition between the triangular proximal portion and the remainder is marked externally by the entrance of the ducts of Gärtner into the uterine substance. This is therefore probably the dividing line between that portion of the uterine mucous membrane developed from the uterine portion of the tubes and that developed from the utero-vaginal canal. These three portions are taken to correspond with the body of the uterus, cervix and vagina respectively, and later, histological evidence in support of this is given.

The Fallopian Tubes. From the reconstruction the tubes differ somewhat in measurement. That on the right is 1·12 cm. in length and varies in breadth from 0·02 to 0·08 cm.; the fimbriated extremity makes up 0·14 cm. of its length. The corresponding measurements on the left are 0·92 cm., 0·02 to 0·04 cm. and 0·14 cm. Both tubes pass outwards until opposite the lateral extremity of the ovary they curve upwards and finally terminate by a distinct inclination backwards, thus ending behind the ovary. Each tube possesses a canal patent throughout its entire length. The lining epithelium consists of cells whose protoplasm stains deeply. The nuclei are oval, intensely stained and large relative to the size of the cells. In places the epithelium is in the form of a single layer which is definitely columnar in parts. In places no epithelium is recognisable because the walls of the tube are almost in apposition; but a potential lumen is always apparent.

The lumen in its simplest form in cross-section has the appearance of a four-rayed star. In this specimen the two ventral and the two dorsal folds producing this formation are not (as described by Felix (1) in Keibel and Mall in a 50 mm. head-foot length embryo) due almost entirely to difference in height of epithelium, but at this stage are formed of embryonic connective tissue. Towards the outer end of the tube, besides these primary folds, there are secondary ones varying in size and shape.

Regarding the remainder of the wall of the tube, the two coats are distinct which Felix (1) describes in a foetus of 80 mm. trunk length. In my specimen, however, they are approximately equal in thickness. Muscle fibres in the adult sense cannot be recognised. Both coats are well vascularised. The inner has irregularly arranged cells with faintly stained protoplasm and oval deeply stained nuclei. The spindle cells of the outer coat form circular layers. The two coats become ill-defined as they are traced towards the outer end of the tube. The inner coat I regard as the forerunner of the stroma of the mucosa and the outer band as destined to form the muscular layer. This is in agreement with Felix (1) and, in the case of the outer band, with Bryce (2), who, however, makes no statement as to the fate of the inner coat.

The tissue of the entire tube is not sharply demarcated from that of the broad ligament. In the boundary zone between run the main vessels of supply to the tube. Near this, the layers, recognisable as serous and subserous by Felix (1), cannot be made out.

Caudal to the mesovarium the common urogenital mesentery passes for-

wards and distally to fuse with the connective tissue surrounding the inner end of the tube. Its point of attachment is about 2 mm. lateral to the median sulcus on the cranial aspect of the body of the uterus. The future body will therefore come to include the inner 1 mm. of the present Fallopian tube.

The Body of the Uterus. Regarding that part of the uterus proximal to the level at which the ducts of Gärtner enter, we find that the anterior and posterior walls are relatively thick. The walls are formed by a continuation of the two coats already described in the wall of the tube. At this level they become widely separated by a third zone which makes up a considerable thickness of the wall. In this, densely packed clusters of cells are found. The nuclei of the cells of this zone are directed for the most part at right angles to the cavity of the uterus. Into this zone strands of cells turn inwards from the outer circular zone. The presence of these strands suggests that this middle zone represents part of the muscular coat of the fully formed uterus. No sharp demarcation exists between these three portions of the uterine wall. No fully formed smooth muscle bundles are present, but the nearest approach to this is found in the circular zone. Nagel (3), (4) found smooth muscle arranged in bundles in embryos of 15–22 cm. length. This muscle appeared first under the peritoneal coat.

The cavity enclosed by these walls forms in transverse section a narrow wavy slit as the anterior and posterior uterine walls are for the most part in apposition. The epithelial lining is similar to that in the tube, although again it is absent in places.

The Cervix. This part, besides being marked off by the relative uniformity of the width of its cavity and by the width of its lateral walls (fig. 3, *B*), differs from the body in some details. This portion, instead of forming an oval in transverse section, is almost circular. The arrangement of the cells of the middle layer of the wall is more irregular than in the body. The increase in depth of the wall of this part is due to an increase in the outer two layers of the wall, i.e. in those layers which will go to form the muscular coat of the cervix.

The epithelium lining the cervix is similar in appearance to that present in the tube and body of the uterus, and here also at certain levels is absent. In the middle line into the upper part of the cervical canal there is a longitudinal bulging of the anterior wall. Opposite this prominence there is a longitudinal groove in the posterior wall. This prominence represents possibly the first commencement of the arbor vitae. No evidence is found in this specimen of the secondary folds of mucous membrane, which are described by Felix (1) as arising from the base of depressions in the wall of the cervix in embryos of about 150 mm. The lower end of the cavity of the cervix forms a narrow transverse slit.

The Vagina. Distal to this portion having a narrow slit-like lumen, there is a sudden widening of the genital canal, and a thinning of the walls (fig. 3, *C*). This foetus resembles those described by both Van Eckeren (5) and Mihalkovicz (6). These observers considered that this dilatation was the first sign of

division into vagina and uterus. Van Eckeren described it as occurring in the second half of the fourth month. Mihalkovicz found a slight dilatation below the position of the external os, even in an embryo 14 cm. long. On the other hand, Nagel (3) described the first beginning of formation of the portio as an ingrowth of the cubical epithelium into the hind wall. He found this in an embryo of 12 cm. length, but in one of 14–15 cm. trunk length it did not occur. This is an example of the variation in time at which the portio develops. Other observers bring evidence in support of this variation. Dohrn (7) described the anterior lip in embryos of 15–16 weeks as a halfmoon-shaped prominence on the anterior wall of the genital tract. Tourneux and Legay (8) described embryos of 12·5 and 16 cm. trunk length in which the portio is present, whereas in one of 20 cm. trunk length he found only the anterior lip. Geibel (9) found the formation of the posterior fornix occurring only in the 6th month, no anterior fornix even then being present.

Just as in the more proximal portions of the genital tract, in this specimen the cavity is lined by epithelium, but at various levels it is absent. The epithelium is stratified and non-vesicular. The nuclei of the cells are oval and small relative to the size of the cell and are rich in chromatin. It may now be noted that the character of the epithelium has been of no value in locating the exact limits of the different regions of the tract.

The structure of the remainder of the wall of the vagina differs from that of the uterus. At the junction of the cervix and vagina the circular layer described in the cervix becomes very thin. Traced distally it soon disappears as a distinct layer. Otherwise the wall is formed of cells arranged irregularly, although the majority of them run longitudinally, especially in its proximal portion. About 2 mm. from the distal end of the vagina, the urethra becomes intimately associated with the anterior wall, so that the one mass of tissue appears to embrace both structures. The vagina tapers down to end in a short solid portion. Gland-like projections of the epithelium of the urogenital sinus pass into this. This distal solid portion of the vagina, for the length of about 1 mm., is enveloped in a band of tissue, like that of the wall of the urethra. The cells of this tissue stain more deeply with eosin than do those of the wall of the vagina.

That portion of the wall intervening between the distal end of the vagina and the cavity of the urethra is made up of interwoven bundles of cells. In the distal 2 mm. of this are embedded branching tubules communicating with the urethral canal and lined by epithelium similar to its epithelium. These tubules I regard as representing the prostate gland in the male, which agrees with the finding of Evatt (10) from the examination of a $3\frac{1}{2}$ months old female foetus, and of Keibel (11), (12) who found the openings of these glands similarly situated. On the other hand, Evatt quotes Gustav Pallin (13) as having found their ducts opening neither into the urethra nor into the vagina, but exactly at the boundary between the two. Around these tubules, in my specimen, spindle-shaped cells are arranged concentrically. In the antero-lateral wall of

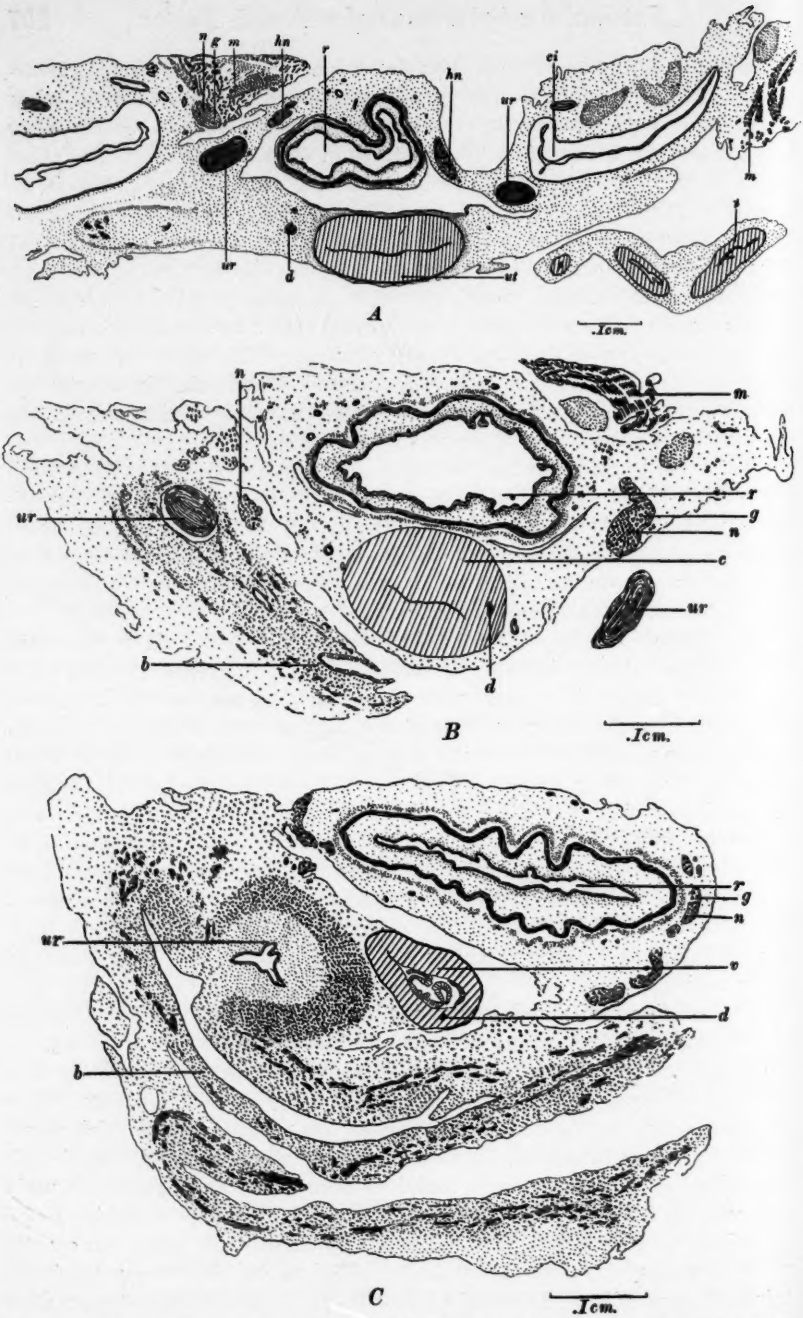

Fig. 3. *A*, transverse section no. 871: for level see fig. 2. *B*, transverse section no. 1159: for level see fig. 2. *C*, transverse section no. 1486: for level see fig. 2. *b*=bladder, *c*=cervix, *ci*=common iliac artery, *d*=Gärtner's duct, *g*=ganglionic nerve cell, *hn*=hypogastric nerve, *m*=striped muscle, *n*=nerve bundle, *r*=rectum, *t*=Fallopian tube, *ut*=body of uterus, *ur*=ureter, *v*=vagina.

the urethra only one tubule is seen and it does not penetrate far into the wall of the urethra. The wall of the urethra is thickly beset with minute venous spaces, especially on its antero-lateral aspect.

REMNANTS OF THE WOLFFIAN SYSTEM AND JUNCTIONAL TUBULES

A. In the mesosalpinx, hilum of the ovary, and common urogenital mesentery, there is on either side a number of tubular structures. They lie proximal to the horizontal part of the tube and posterior to the ovary.

The majority of the tubules are clustered together to form the epoöphoron which lies lateral to the mesovarium. Opposite and medial to the mesovarium, scattered tubules are found. The tubules are sinuous in their course. Each is cylindrical, lined with a single layer of cubical epithelium placed upon a basement membrane. The nuclei are large and deeply stained. The epithelial tube is surrounded by a condensation of primitive connective tissue cells. There is an inner coat longitudinal in arrangement and an outer ill-defined coat of circularly arranged cells. One of the more lateral of the tubules is distinguished by its larger lumen and by its thicker connective tissue wall. This is the remnant of the Wolffian duct. It runs more or less parallel to the lateral portion of the Fallopian tube. No muscle cells are seen either in the walls of the Wolffian tubules or of the duct.

Two other types of tubules are found:

(*a*) The first is a goup of tubules lined by cubical epithelial cells with deeply stained nuclei. Each is surrounded by a very thin connective tissue coat, the cells of which are arranged circularly. The tubules differ from those of the epoöphoron in having no well-defined longitudinal connective tissue coat. They lie medial and posterior to the ovarian artery in the common urogenital mesentery where it is reflected on to the posterior abdominal wall just lateral to the ureter. In this specimen they are better developed on the right than on the left side. One of the tubules is distended with epithelial débris, its contents staining deeply with eosin. The distended part is 0·12 mm. in length. Some of these tubules are replaced by solid cords of cells. No blood-vessels are seen in these cell-clusters. The difference between this connective tissue wall and that of the tubules of the epoöphoron may result from a difference in their stage of retrogression. Whether these more medial tubules represent the paroöphoron cannot be judged from the study of an isolated specimen. Duthie (14) failed to demonstrate the paroöphoron in all twenty specimens examined. Felix (1) quotes Waldeyer (15) as having described it in a position cranial to the medial pole of the ovary and Rielander (16) in older foetuses and children caudal to the lateral half of the ovary. In my specimen these tubules lie cranial to the hilum of the ovary.

(*b*) The second type occurs in the region of the ovarian fimbria. Each tube ends blindly and has a cavity irregular in outline. Three are present on the

right side, one being in the hilum of the ovary and the other two nearer the tube. The one on the left side lies in an isolated projection from the posterior surface of the ovarian fimbria. No connection can be made out between them and the Wolffian duct and tubules. Each is lined with low cuboidal epithelial cells and is surrounded by a very thin condensation of connective tissue cells arranged circularly.

No smooth muscle fibres are seen in their walls. Duthie (14) describes similar spaces in a human foetus of the 8th month. They probably correspond to the rete or junctional tubules of Allen (17). If they are rete or junctional tubules, the tissue in which they lie must be ovarian or hilum tissue which has made its way up the ovarian fimbria. Keith and Doran (18) describe the ovarian tissue as running some way up the ovarian fimbria in a human foetus of the 8th month and in the new-born child. The facts that no connection can be made between any of them and the lateral end of the Wolffian duct and that their walls differ markedly from that of the Wolffian duct are against their being remnants of the pronephric duct.

B. Within and near the lower portion of the genital tract are remnants of Gärtner's duct. Meyer (19) found such remnants of Gärtner's duct in the uterus in all specimens at the stage of 2–3 months' development, but only in 28·5 per cent. of specimens aged 4–6 months. On both sides (fig. 2) portions of Gärtner's duct are seen. On neither side can a connection be traced between these and the other remains of the Wolffian system in the lateral parts of the mesosalpinx. At their proximal end both appear as an ill-defined condensation of the connective tissue of the broad ligament. The duct on the right side begins at section 880 and can be traced down to section 1235. It lies about 0·4 mm. lateral to the wall of the uterus, surrounded by tortuous veins and just posterior to one of the branches of the uterine artery. Passing distally, it approaches the uterine wall. As it does so, its tissues become differentiated into an outer condensed and an inner loose zone. About 1 mm. from its commencement this central loose zone is replaced by the cavity of the duct, which is lined by a layer of deeply staining cubical epithelium. The cells of the outer condensed zone are arranged concentrically. Peripheral to this latter zone, no distinct layer of longitudinally arranged cells, such as was found by Meyer (19), can be made out in this specimen. The duct becomes closely applied to, and eventually enters the wall of the genital tract, where the thin lateral wall of the future body thickens out to form the wall of the future cervix. As the duct is traced distally within the wall, its lumen enlarges antero-posteriorly and the epithelial lining assumes a columnar form. Its condensed band of connective tissue remains distinct from the tissue surrounding it, not only because of the concentric arrangement of its cells, but also because of their smaller size. As it passes down the cervical wall its cells become less regular in arrangement, so that it is less sharply marked off from the surrounding tissues. It passes gradually more deeply into the wall, until near its termination it lies completely within the circular layer and bulging the deeper layers inwards.

It ceases to be recognised about 0·04 mm. above the proximal end of the future vagina. This remnant in this part of its course is 3·5 mm. long.

On the left side the duct is much shorter. It appears first in section 862, lying in close apposition to the uterine artery about 3 mm. lateral to the wall of the uterus. As in the case of the right duct, no connection with the other vestigial structures in the broad ligament is established. As it is traced distally, it has the form of a poorly demarcated collection of cells with deeply stained rounded nuclei. A concentric arrangement of cells is only seen (fig. 3 A) opposite the minute epithelial lined cavity 0·02 mm. long. The duct cannot be traced beyond section 968, where it merges with the wall of the utero-vaginal canal. The left portion of the duct of Gärtner thus measures only 1 mm. in this part of its course.

On neither side is there any trace of Gärtner's duct in the walls of the proximal half of the vagina. In the distal half on the right side two portions of the duct are found, the proximal one, 0·1 mm. in length, possessing a lumen lined by columnar cells, and the distal, 0·04 mm. in length, having only a solid epithelial core. Both are placed in the antero-lateral wall of the vagina, but their position in the length of the vagina is represented in fig. 2. Between these two portions traces of the wall of the duct can be seen. On the left side the three portions, 0·04, 0·03, 0·02 mm. in length respectively, each possess a lumen lined by epithelium. On neither side are any remnants found at the distal extremity of the wall of the vagina, and no communication is established between the portions of the duct present and the glands opening dorsally from the urethra (cf. Kocks (20) and Böhm (21)). In this specimen, just as in those described by Rieder (22) and by Dohrn (23), the duct of Gartner has been retained more upon the right side than upon the left.

SYMPATHETIC NERVE DISTRIBUTION

The work of Langley and Anderson (24), (25) has shown that the nerve fibres supplying the uterus and the vagina pass chiefly by the sympathetic in the region of the fourth, fifth and sixth lumbar ganglia. Langley and Anderson (26) showed that a variable number of these fibres formed cell stations in the inferior mesenteric ganglia, and that many, and occasionally all, passed by way of the hypogastric nerves into the more peripheral nerve cells. The position and relations of these nerve cells and their morphology are still imperfectly known. On the course of the hypogastric nerves, Langley and Anderson (27) describe in the cat groups of ganglionic cells on the hypogastric nerves near the cervix, and in the rabbit similar cells at the lateral border of the vagina. From these they find a ganglionated plexus stretching along the vagina. In the guinea-pig Holste (28) found groups of ganglionic cells at the level of the cervix in the supravaginal connective tissue. Labhardt (29) reports that in the human subject Koerner and Polle both describe ganglia in the connective tissue around the upper half of the vagina

and the cervix, and that Pissemski, having found a plexus of nerves with ganglia scattered along it, denies the existence of an individual cervical ganglion such as described by Walter, Lee, Frankenhauser, Hashimoto and Jung. More recently, also, Mabuchi (30) has described two lateral, two ventral and a dorsal ganglion at the level of the cervix. As J. Ogata, according to Mabuchi, has shown that ganglionic cells had developed in the uterus, even in a foetus of 4 months, it was considered that valuable information on this subject might be obtained, if the position of these groups was found in a foetus of about 4 months, when the internal genital organs are sufficiently small to permit of

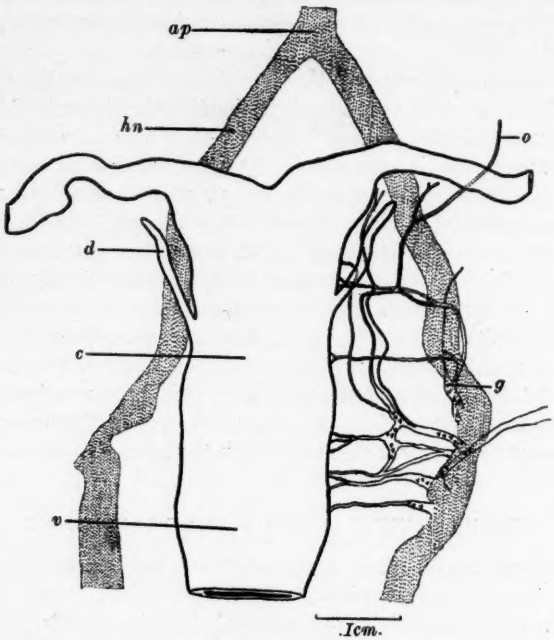

Fig. 4. Flat reconstruction of the nerves from the serial sections. *ap* = aortic plexus, *c* = cervix, *d* = Gärtner's duct, *g* = position of ganglionic nerve cell, *hn* = hypogastric nerve, *o* = nerve to the ovary, *v* = vagina.

a complete series of sections being made. Only in a specimen from a young foetus can sufficient of the broad ligament be included in the sections to permit the localisation of these ganglia.

A graphical reconstruction (fig. 4) has therefore been made from this specimen to show the branches of the hypogastric nerve to the uterus, and the position of the groups of ganglionic cells on these branches. The series of sections extended to the inferior mesenteric ganglia, from which bundles of nerve fibres pass to the intestine along with the inferior mesenteric artery.

A median plexus of nerve fibres runs distally anterior to the aorta. The last-named (fig. 4) divides about 2 mm. distal to the fundus of the uterus, to form the hypogastric nerves, along the course of which ganglionic nerve cells are scattered. They are most numerous opposite the cervix in those parts from which the branches supplying the uterus and tubes arise. The hypogastric nerves lie about 0·2 mm. lateral to the wall of the uterus.

On the course of the most proximal of the branches of the hypogastric nerve is a mass of ganglionic cells. This branch passes upwards and anteriorly, giving off a transverse branch to the cervix. Continuing its course it divides into two branches which run to the cervix at the level of the future internal os. From these transverse branches bundles of nerve fibres run upwards, to supply the upper part of the body of the uterus and the tubes. From the more lateral of these divisions a small branch is given off which passes into the hilum of the ovary. The original two branches, running to the uterus at the level of the internal os, communicate with the more distal branches of the main hypogastric nerve by lateral communicating unions in the broad ligament, which lie within 0·1 mm. from the wall of the cervix. The more lateral of these two lies behind the other.

Coming back now to the first branch of the hypogastric nerve mentioned above, about 0·5 mm. distal to it a second ganglionated branch runs transversely towards the cervix, and, as described, communicates with the branches already distributed to the uterus. This particular nerve shows two branches, one of which terminates at the middle of the cervix, and the other at the internal os. Another main branch is given off the hypogastric about 0·6 mm. distal to and communicating with this second branch. This branch comes off below the level of the peritoneal reflexion posteriorly. It supplies the lower part of the cervix, and sends a large branch laterally anterior to the ureter. This latter subdivision has ganglionic cells upon its course and distributes branches to the bladder. Further distally two other branches of the hypogastric, supplying the lower end of the cervix, can be traced to the wall of the cervix. Excluding the first branch of the hypogastric, the communicating branches of which have been described, the remaining branches communicate with one another in an irregular manner.

It was found impossible to trace out the more distal branches supplying the vagina, as they are in such intimate association with the branches both to the rectum and to the urethra and bladder. The connections between the hypogastric plexus and the spinal nerves were necessarily destroyed during the removal of the vertebral column. In this specimen, therefore, the ganglionic cells are not confined to form a single cervical ganglion, but are scattered along the divisions of the hypogastric plexus in the region of the cervix.

Let us consider now what light this specimen thows upon the question as to whether ganglionic cells occur only on that part of the course of the fibres of the hypogastric nerves outside the uterus, or whether ganglionic cells are also present within the substance of the uterine muscle. Much work has been

done, using all the commoner special nerve stains, and yet opinion is divided. According to Mabuchi (30), Körner, Polle, Henle, Lüschka, Spiegelberg, Hashimoto, Jung, Ogata and Krause, only describe ganglia in connective tissues near the cervix and vagina; and Kilian, Röhrig (31), and Rein (32) failed to find any ganglia in the uterine substance. Dahl (33) has been unable to find ganglionic cells in the human subject, either in the mucous membrane or in the muscle of the uterus and tube. On the other hand, Gawronsky (34) described ganglion-like formations in the uterine parenchyma, such as had been found by Patenko, Kolossoff, Schenk and Herff. In the case of cells resembling ganglionic cells found by Clivio, Köstlin, Spampani and Mabuchi (30) within uterine muscle, their nature was not proved, as their connection with nerve fibres was not made clear. Keiffer (35) reports the presence of small ganglionic cells within the uterine wall of the cat and the guinea-pig. In this specimen, no cells similar in size and shape and staining reaction to the ganglionic cells on the hypogastric nerves outside the uterus were found within the wall of the vagina, cervix, body or tubes. While the majority of the sections were stained with haematoxylin and with eosin, a series at intervals was stained by a modification of the Unna-Pappenheim method of staining, the methylgreen-pyronin method used by Hynntschak (36). Although these stains showed up the larger bundles of nerve fibres within the uterine muscle, the smaller bundles and individual nerve fibres could not be traced between the cells forming the wall of the uterus. It is therefore impossible to say definitely that no small ganglionic cells are present within the uterine wall, but one can almost certainly exclude the presence of ganglionic nerve cells similar in character to those found on the course of the sympathetic nerves outside the uterus.

CONCLUSIONS

(1) No muscle fibres are found in the tubes, the walls of which are composed of primitive connective tissue. Two zones of cells can be made out. The inner ones are irregularly arranged and the outer ones are larger, more deeply stained, and arranged in concentric circles.

(2) No trace of a median septum between the portions of the uterine cavity developed from the two tubes is found.

(3) The unpaired portion of the internal genital tract is divisible into three parts: (*a*) a proximal triangular portion with thin lateral and thick anterior and posterior walls—the future body of the uterus, (*b*) a middle narrow portion, having a circular outline—the future cervix, and (*c*) a long tapering relatively thin-walled portion—the future vagina, which ends in a short solid mass, abutting on the cavity of the urogenital sinus.

(4) The transition from the cervix to the vagina occurs as a sudden widening of the genital canal under a narrow slit-like portion—the external os. At this stage no projection into the vaginal canal which would represent the portio vaginalis is present.

(5) Glands corresponding to the prostate gland are found in the postero-lateral wall of the urethra, adjacent to the distal 2 mm. of the vagina.

(6) That part of Gärtner's duct within the wall of the uterus and vagina, is better preserved on the right than on the left side. A slight dilatation which would represent the ampulla of the duct is seen on the right side.

(7) There are no muscle fibres in the wall of the uterus, cervix or vagina although they are present in the wall of the bladder, urethra, and urogenital sinus.

(8) The sympathetic nerve fibres, supplying the internal genital organs, pass down the hypogastric nerves to the level of the cervix, and then pass to the tubes, uterus, cervix and upper portion of the vagina, by several branches which communicate with one another. These branches are intimately associated with branches of the uterine artery.

(9) Ganglionic cells are scattered along the hypogastric nerves and occur on each of their main branches, but only on that part of their course opposite to the cervix and vagina.

(10) Within the wall of the genital tract, no cells comparable in size, shape or staining reaction to the ganglionic cells found on the more proximal portions of the sympathetic nerve fibres, are seen.

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INTRA-MUSCULAR NERVE ELEMENTS OF THE VENTRICULAR MUSCLE

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In a recent paper, Boeke(1) repeats the statement of Mollard(2) in 1908, "qu'à l'heure actuelle on ne connaît pas encore d'une façon certaine et définitive le mode de terminaison des nerfs dans le myocarde. L'existence de terminaisons motrices établies sur le type de celles les plus simples des muscles striés ordinaires (Renaut) n'est pas démontrée, non plus que l'existence d'un type spécial de terminaisons différentes à la fois de celles des muscles striés qui sont enveloppées dans un sarcolemme, et de celles des muscles lisses (Smirnow)."

The histological investigation of the innervation of the cardiac musculature has, indeed, offered hitherto insuperable difficulties, which Boeke, who has worked at this problem for years unsuccessfully, is at pains to emphasise. The nearest approach to the solution of the problem until the appearance of Boeke's paper lay in Gerlach's observations published in 1876(3). Ranvier, it is true, later asserted that the nerve fibrils actually penetrated within the substance of the muscle cells, and there passed to the neighbourhood of the nuclei. Attributed to defective technique, and wholly uncorroborated, these statements have been neglected in recent discussions. In the absence of knowledge of the ultimate destination of the cardiac nerves attention has been concentrated upon the possible modes of operation of a retiform innervation, the distribution of ganglia in the heart wall and their connections with the cardiac nerves. Many workers, overcome by the weight of evidence in favour of the myogenic theory of the origin of the heart-beat, assumed, quite unwarrantably, that the cardiac nerves, so far as the musculature was concerned, produced their results through the intermediation of the nodal tissue alone, and that any wider distribution they might have was purely vaso-motor. It is interesting to recall the care with which Lewis(4) in his masterly work on the mechanism of the heart-beat avoided this assumption, insisting that the question was still unsettled.

In his brief review of previous work, Boeke refers to the observations of Gerlach in these terms: "As it was described already years ago by Gerlach, the nerve-fibres of the heart-wall form everywhere a network, a plexus. Large nerves do not enter into the heart-muscle, except the larger nerve-branches,

...which originate from the groups of ganglia in the septum atriorum and the neighbourhood of the large veins of the heart and pass from here to the wall of the auricles and of the ventricle. The ramifications of these nerves form a dense nerve-plexus under the endocardium (the 'groundplexus' of Gerlach and Hoffmann)." But this by no means reveals the whole extent of Gerlach's discovery or its amazingly close approach to those of half a century later. Not only did this writer describe the "ground-plexus" attributed to him, but he made further observations which may still assume the greatest importance for our understanding of the nature of muscle and nerve. "In the heart of the frog," he says, "there are three nerve endings: (1) a ground-plexus which is formed of both coarse and fine fibres and contains ganglion cells; (2) a peri-muscular net which spins around the individual muscle-fibres. It is formed of finer fibres which show varicosities in their course and at the junctional points; (3) an intra-muscular net consisting only of nerve-fibrils which run in the centre of the muscle bundles, between the cells, and which may penetrate into the substance of the muscle cells ("welche in das Innere der Muskelzellen eindringen können"). A drawing and its subscribed description, however, leave no doubt as to the interpretation which Gerlach intended to be placed upon these words: he meant penetration into the muscle syncytium, and in complete conformity with this he writes: "Wir müssen dahin gestellt sein lassen, ob der Name Nervenendigung überhaupt gerechtfertigt ist, ob nicht ein continuirlicher Uebergang von feinster Nerven in die contractile Substanz existirt, so dass die Muskelfaser selbst als Nervende zu betrachten wäre."

Boeke's contribution to the discussion of important new evidence will be examined presently. As it is the purpose of the present paper to corroborate and extend the scope of his observations in certain particulars, attention will be confined to the histological points at issue. For recent reviews and bibliographies, the reader may be referred to the published work of Mollard (2), Einar Perman (5), Fukutake (6), Glaser (7) and Ernst Edens (8).

Boeke, using the Bielschowsky method with somewhat prolonged impregnation in the $AgNO_3$-solution, claims to have succeeded in getting "good preparations with an excellent and elective colouring of the nerve-fibres and their endings in the cardiac muscle of the heart of tortoises and birds, and with tolerable results in the heart of the hedgehog." In the communication under review, however, he confines himself to description of the nerve-fibres, the relations of the nerve-fibres and their terminal ramifications with the muscular elements, and the innervation of the muscular elements of the atrio-ventricular connection (bundle of His), in the heart of the tortoises (*Emys europaea*, the European pond-tortoise, and *Cyclemys* sp.), "because with those hearts I obtained the best and most complete results." I may summarise the two chief results of this investigation by saying that, in the heart of the tortoise, Boeke claims to have found everywhere in the cardiac musculature an innervation of the individual contractile elements not only by a pericellular network

without definite nerve-endings, but by very fine, varicose branches, which pass into the muscle-cells and lie imbedded in the protoplasm itself, where they end in small end-nets or end-loops, or "a series of terminal varicosities appearing as very small ring-like expansions of the neuro-fibrillar structure." At times, however, instead of ending abruptly in this manner, the fine fibrils may be followed through several "cell territories" before terminating. He finds the bundle tissue similarly innervated. These findings are illustrated by a few, very clear drawings. Boeke states, further, that "the delicate varicose neurofibrillar threads furnished with end-rings and end-loops, whose intra-protoplasmic position could be made out convincingly, showed here and there a distinct connection with the sarcoplasm, an extremely delicate network, at one side continuous with the neurofibrillar structure, at the other side apparently passing into the cross-striation of the myofibrillae, at least with meshes, which in size correspond with the width of the cross-striation." It is unfortunate, in view of the rather vague and confusing presentation of this important matter here given, that the appearance referred to is not illustrated in Boeke's paper. But to this reference will be made later.

ORIGINAL INVESTIGATION

The chief method adopted was that of intra-vitam injection of a solution of Methylenblau BX (Grübler) to the strength of 0·02 per cent. in 0·75 per cent. saline.

The animal, a cat, was anaesthetised and the left common carotid artery exposed. The injection was then made under a pressure of about 200 mm. Hg into the proximal end of the cut artery, the distal end being tied. As the fluid began to enter, the right jugular vein was clamped and cut distally to the obstruction. Injection was continued for three minutes after the stream from the vein became coloured, as this occurred almost immediately owing to escape through the unobstructed right carotid artery. After death the animal was treated in the usual way in this method, and after dissection of the tissues they were fixed in ammonium molybdate 8 per cent. solution in the cold. Dissection consisted in stripping portions of the visceral pericardium and in removing from the underlying ventricular wall strips as thin as possible of the muscle substance cut in the long axis of the cells. Elsewhere, thin transverse sections—i.e. from without inwards—were made with a razor, each section comprising the whole thickness of the ventricle. The material for study thus included portions of the visceral pericardium, portions of the underlying muscle cut longitudinally and sections from epicardium to ventricular cavity. Some of this material was cleared in benzyl benzoate; some in xylol after further dissection to render it more suitable for observation under high powers. These latter portions were subsequently mounted in xylol-balsam.

It will be convenient to deal with this material according to its mode of preparation:

(1) The pericardium. This material, having been exposed to air longer

than the rest, was very much over-stained and practically useless except for the identification in certain favourable spots of the large nerve bundles adhering to its inner aspect. Unlike Boeke, I have found no exception to the varicose nature of the fibres constituting these bundles; the fibres vary considerably in size, but all are non-medullated and so heavily "beaded" as to give a quite distinctive appearance to the bundles, which, being in addition flat and ribbon-like wherever they appear in the ventricular wall, are not wholly similar to those found anywhere else in the body. In many situations these bundles may be found broken completely across; but nowhere in this situation have I seen any marked tendency to form branches. These circumstances appear to lead inevitably to the conclusion that most, if not all of the fibres forming these nerves are destined to pass internally to the deeper structures of the heart-wall.

(2) The sub-epicardial portions. The staining here showed such variability as to merit special description, particularly because the results to which I attach most importance were secured wholly on account of this variability. It appears that, so far as the heart muscle is concerned, the critical factors in intra-vitam staining—absorption, reduction, oxidation—occur much more rapidly than in any other muscular tissue. Overstaining is the rule, and of a diffuse kind, indicating that oxidation of the reduced dye has occurred too late or has been too prolonged. Reviewing my own procedure, there appear to be three distinct exposures of the tissue to the action of the air: a first on opening the pericardium, a second on stripping the visceral layer, and a third on further dissection. However rapidly these operations are performed, the coloration reaction to the third of these successive exposures is much longer delayed than is that to the second, while a dense blue develops almost instantaneously when the pericardial sac is first laid open. As though in strict keeping with the time factors in this considerable variability in the colour reaction, I find three distinct types of histological staining:

(*a*) A generalised staining of the muscle elements without marked differentiation of their nuclei but with complete obliteration of contiguous nerve filaments.

(*b*) Faint, or granular staining of muscle elements, with heavy staining of the larger nerve fibrils, good staining occasionally of the smaller nerve elements but without differentiation to the slightest degree of the nuclei of the muscle cells. It is this type of staining, I imagine, that has resulted in the occasional past descriptions of peri-muscular nerve nets and of the ground plexus of Gerlach.

(*c*) Faint diffuse staining, or faint granular staining of the muscle, of which the striations appear highly refractile to suitably adjusted illumination, with deep staining of the nuclei and clear staining of nerve elements.

All of these variations occur in my preparations of the sub-epicardial musculature; (*a*) is useless for all purposes, (*b*) is the only mode of staining I have been able to detect in the thicker pieces of tissue cleared by the Spalteholz

method, (*c*) alone affords evidence of the mode of termination of the cardiac nerves so far as the musculature is concerned.

(3) The slices through the whole thickness of the ventricular wall exhibit all the variations in the staining reaction enumerated above. Externally there is dense overstaining which makes study of the involved layers impossible; next is a thin band with stained muscle nuclei; the rest is fairly uniformly stained to show clearly those fine ramifications of the nerves which I take to be the ground-plexus described earlier by various workers. Here also may be seen occasionally the double or treble *anastomosing* fibrils, which, following an irregular but parallel course (if one disregards for the moment the anastomoses) are precisely like vascular nerves elsewhere in the body and are clearly to be identified with such structures.

Boeke has experienced difficulty in deciding whether the branches of the ground-plexus form closed meshes or not. This is a matter which seems to be impossible of settlement from the study of serial sections either singly or in relation to each other. The fibrils are so minute, and their course so irregular that to observe a complete loop within the confined space of a slice even 10μ thick is hardly to be expected; while the superimposition of drawings of these small fibres made from successive sections, however carefully and skilfully, must provide data equally misleading and inconclusive. But several of the slices prepared as indicated in the last paragraph make it possible to view with perfect clearness a continuous series of optical sections throughout a layer of muscle tissue, over a millimetre thick, undisturbed by any mechanical interference whatsoever. It is true that in these preparations the actual terminations of the nerves are not visible; but neither is the number of the ramifying fibrils reduced. It is thus impossible to conclude that anything but the terminations themselves is removed from the picture which these slices present in well-stained areas; and this becomes all the more certain when the peculiar environment of the endings is taken into account, fully explaining, as will be shown later, why they, and they alone, are removed from the influence of the stain.

For these reasons, the picture of the ground-plexus afforded must be accepted as a true one in all its essential particulars. It provided positive evidence that the magnitude of the nerve fibrils is diminished imperceptibly by repeated division; that such subdivision takes place relatively near to the point of termination, each branch travelling for a short distance transversely to the muscular trabeculae and then onwards for as much as ·1 mm. in the direction of the muscle fibres, where it may again turn aside, with or without branching, and end. Isolated nerve cells appear in the course of the nerve bundles. (Fig. G.) In the larger nerve bundles themselves no branching of fibrils can be detected, and the same may be said of the smaller bundles. The size of the bundles is reduced by separation, often at very sharp angles, of the fibres composing them. These bundles, of whatever size, run for very long distances in the ventricular wall, like flattened bands, surrounded completely

by the muscle. In this way the illusion is produced of a continuous nerve network which cannot be related directly to the nerve bundles, an illusion assisted very powerfully by the almost total absence of decrement in the size of the fibres. There is, on the contrary, a perfectly orderly separation of the bundles into their constituent fibres, with a late subdivision of these into branches, which maintain their integrity throughout their course. There is no true net formation. This observation accords completely with all the known facts of the development of the heart. There is nevertheless a true plexus

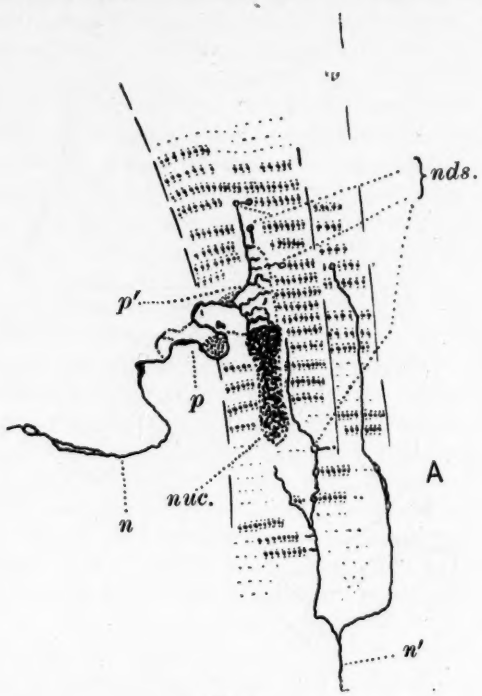


Fig. A.

accompanying the vessels of the myocardium. It has a continuity of its own, although it receives occasional subsidiary branches from fibres running apart. Whether such fibres subsequently supply the muscular elements as well, it has not been possible to determine. Wherever they appear in the ventricular musculature, the nerve fibres are histologically indistinguishable.

The branches behave in the cat almost exactly in the manner which Boeke has described with great clearness for the tortoise, entering the syncytial tissue itself sometimes near their terminations, sometimes at a considerable distance from them. This arrangement is indicated in Fig. A, where both

an early and a late termination of the fibrils after entry into the muscle substance are seen. This intra-protoplasmic course is of exceptional interest and importance, and it is necessary to state the evidences upon which the assertion of its existence rests. Boeke, apparently, has reached this conclusion, with which I am in entire agreement, from two paths. Firstly, he has identified in transverse sections of the muscular trabeculae intra-protoplasmic neurofibrillar endings embedded in the cell-substance near the nucleus. And secondly he has found, in longitudinal sections, loops of the fibrils in such close apposition to the nucleus that they appear to cause an annular constriction

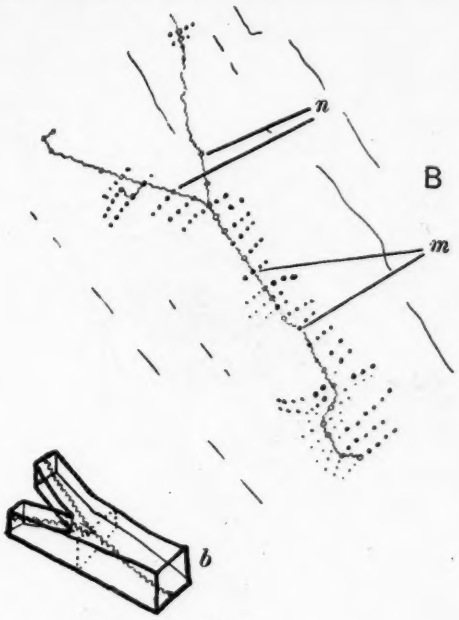


Fig. B.

so deep as to give rise to the impression that two nuclei instead of one are present. Various objections might be advanced against the acceptance of this evidence, and even the identification of certain parts of the nervous apparatus with the substance of the dark cross-striations of the muscle might be possible of misinterpretation from this point of view. My own preparations, however, show many examples of a more complicated mode of termination than that described and figured by Boeke; and I had already, before I became acquainted with his paper, taken other steps which led me to a decision concerning the matter under discussion. Before describing these, I may say that the binocular examination of the structures in question, which so often gives conclusive evidence of vertical relationships, perhaps because of the irregularity of the

muscular features and the extreme differentiation in the intensity of the staining, is not here of great critical value.

In places, however, the muscle substance itself becomes stained, either lightly, giving rise to a finely-granular appearance, or densely, revealing with perfect clearness the familiar light and dark bands which give the muscle its appearance of striation. Intermediate stages are met with, in which the dark bands appear as rows of dark dots, corresponding to the position of Hensen's lines as they are represented in current descriptions of muscular structure. If the muscle fibres are not lying in a plane normal to the optical axis of the microscope, the dots composing each dark band show a marked tendency to shift to one side or the other on focusing, fresh rows of dots constantly

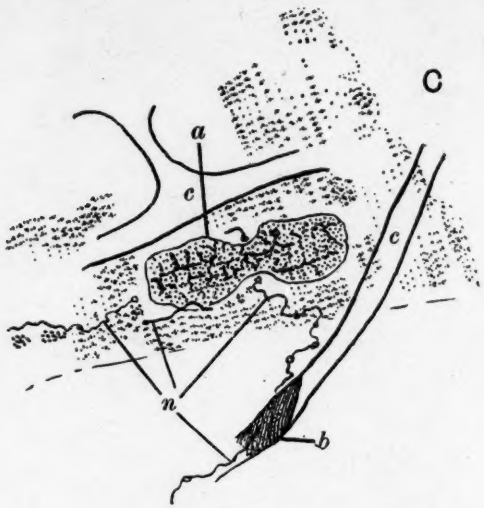
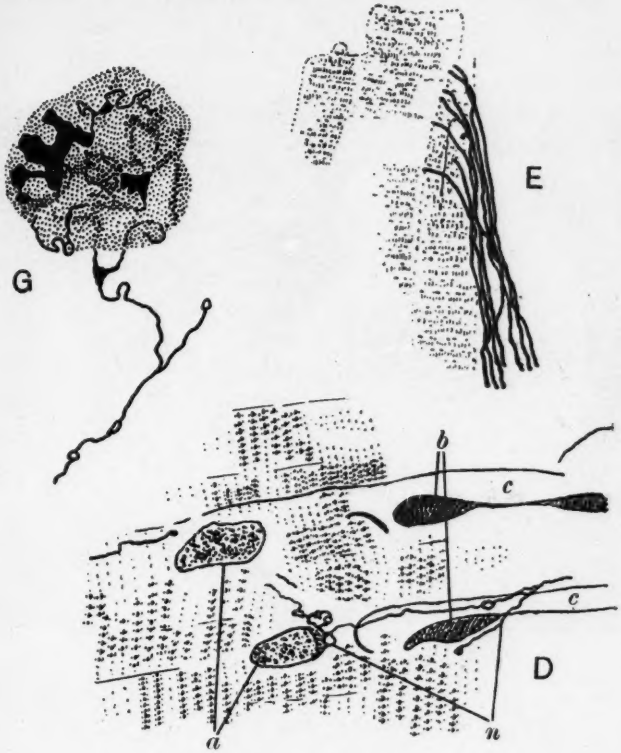


Fig. C.

taking the places of those which pass obliquely out of view. Now, by plotting with the aid of a drawing apparatus first the dark bands in one coloured ink and later the unmistakably nervous elements in another coloured ink, it should be possible to construct a map of the path of the nerve fibrils. I have several times attempted to follow this plan, and have in no instance found the slightest divergence from the rule that certain typical markings along the course of the nerve fibrils assume positions which should be occupied by portions of the dark bands. These nervous markings are the small varicosities or loops or rings—small dark swellings with clear, lightly-refracting centres—seen on the nerve fibrils of my figure (Fig. A); while in Fig. B I have reproduced one of the results obtained from this method of double drawing, with a diagram illustrating the path of the fibril through the muscle substance. From the

varicosities which I have described, and from neighbouring situations along the fibril, where there may or may not be present others of these tiny nodes, continuations of the fibril may pass horizontally along Hensen's line to end in the minute enlargements typical of this part of the nervous apparatus, the main fibril passing onwards in the myofibril.



Figs. D, E, G.

The intimate relationship of the terminal apparatus to the nucleus is clearly indicated in my figure (Fig. A). Whether the relationship is one of contact, or of investiture, or merely of contiguity it is impossible to decide by reference to the heart preparations alone. There seems no reason why in this respect the nuclei of heart muscle should differ from those of skeletal muscle, and there I have repeatedly observed apparent continuity between the nuclear network and prolongations of the "nerve-ending" in preparations made by Ranvier's gold-chloride method. Such an appearance is reproduced in Fig. F—a microphotograph of an "end-plate" (as it is described by Kühne) from M. gastrocnemius of the cat. In this preparation are shown with perfect

distinctness two nuclei of the "sole-plate" in close apposition to the embracing arms of hypolemmal processes from the axis cylinder. While the photograph is incapable of reproducing the differential staining of the original preparation (gold-chloride—haemalum), it nevertheless shows with perfect distinctness the relation between the nuclear chromatin and the neural structure. In the heart muscle, the nature of the association is disguised by the peculiar staining of the nuclei; but the association itself is a striking and remarkable feature of several examples of endings which I have studied.

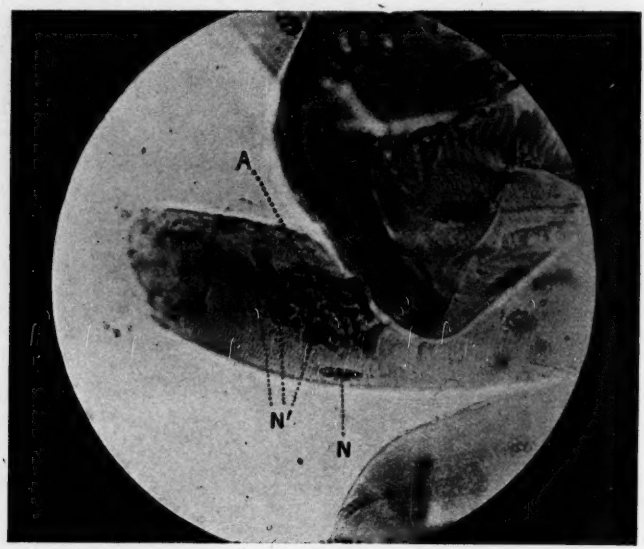


Fig. F (× 1000). From a microphotograph by Mr J. R. Bell.

Before proceeding to summarise these results, I may give a brief account of an examination of the posterior papillary muscle of the left ventricle in the human subject. The histological material was prepared at the end of 1924 by Ranson's pyridine-silver method, from the heart of a young female insane patient, whose heart muscle was found, post-mortem, to be healthy. The drawing (Fig. E) was made at this time. It shows a bundle of eight nerves proceeding in the direction of the muscle fibres towards the apex of the papillary muscle, and from one of these a minute fibril descending on or in the muscle. Failing further to elucidate the ultimate destination of the nerves at this time, I set the material aside. Re-examined, however, in the light of knowledge gained from the cat's heart by intra-vitam staining, I find abundant evidence of the existence of a similar arrangement to that which I have described for the cat. The staining is bad, and, owing to sectioning, the nerve elements can be

viewed only in fragments; yet their form, arrangement and distribution renders them now unmistakable. The relation of the small rings of the fibrils to the dark bands of the muscle, and of the more complicated ramifications to the nuclei, is as marked as in the cat. Drawings of some of these fragments are shown in Figs. C and D.

CONCLUSIONS

To sum up what I consider to be the established facts relating to this mode of innervation. The nerve fibrils of the myocardium enter the muscular syncytium, and there form endings which replace recognised histological units of the contractile elements. They may, additionally, establish a relationship of the closest intimacy with the nucleus. The fibres of the more complicated endings of this type enter the muscle substance near their terminations, form a small plexus external to their point of entry and another internally, from which terminal branches proceed. It is impossible to say whether the two modes of termination here described are functionally the same or different.

It is possible, without departing from the terms of direct observation, to present the facts of the association between nerve and muscle in an intelligible form. Boeke says "there is a distinct connection with the sarco*plasm*[1]." The intramuscular network, as I have seen it, occupies one pole of the undifferentiated perinuclear protoplasm. Its longitudinal branches are irregular in their course, which, in part, at least, lies through the less differentiated substance—protoplasm or sarcoplasm. In part these branches or their ring-like nodes appear to *take the place* of the most highly-differentiated protoplasm of the muscle.

While it is wholly unwarrantable to state the observed facts in any terms but these, a brief reference to past controversies is unavoidable, particularly in view of the increasing evidence in support of the continuity theory of neurofibrillar intercommunication. Not only has the existence of a primitive protoplasmic bridge, representing the motor trunk at a time when myotome and spinal cord have not yet commenced to move apart, been demonstrated for Lepidosiren by Graham Kerr (10), but this has been confirmed in the case of the motor trunks of Elasmobranchs by Paton (11) and in the case of the olfactory nerve of various vertebrates by Elliot Smith (12). Bethe (13) long ago asserted the continuity of the neurofibrils of contiguous neurons, and Miss Ballantyne (9) has recently made an exhaustive study of *Lepidosiren paradoxa* from this point of view and has added to previously existing evidence of con-

[1] Boeke's previous work does not throw much light on his meaning here, for he says: "I know of only one case in which the neurofibrillar structure (or something akin to it) is found to be continuous with the myofibrillae. That is in amphioxus....In all other vertebrates there lies...a stretch of undifferentiated granular sarcoplasm between the terminal ramifications of the neurofibrillae and the contractile substance, the myofibrillae."—*Brain*, XLIV, p. 13, 1921.

tinuity important facts relating to Lepidosiren[1]. The demonstration of neuro-myofibrillar continuity is thus in harmony with the illuminating conception advanced by these workers.

The view that the intra-muscular fibrils end in the sarcoplasm is contradicted by their terminal assumption of positions proper to elements which have hitherto been considered as essentially contractile. (Cf. Tonus of Skeletal Muscle, Review by Stanley Cobb: *op. cit.*(14)). The embryological evidence

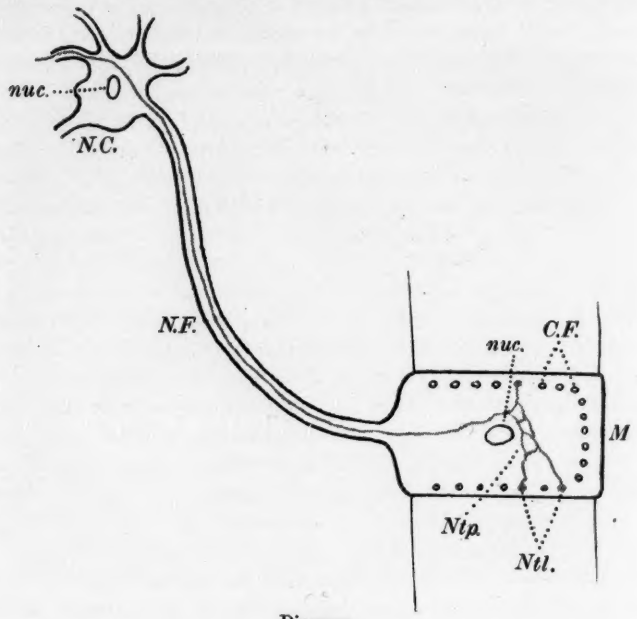


Diagram.

still further associates the nerve fibrils with the parts of the muscle protoplasm specialised for contraction, for, just as the nerve fibrils develop in the substance of the nerve, so do the contractile elements undergo formation from the undifferentiated protoplasm of the developing muscle cell. The muscles, as Gerlach said, are the "contractile endings of the nerves": they alone are nerve endings.

The diagrammatic form into which I have thrown these facts (Diagram) thus not only expresses my observations of the course of the nerve elements faithfully, but summarises the hypothesis I put forward in brief outline to explain the intimate structure of muscle. While this proceeds directly from

[1] Observations under different conditions of staining of the ganglionic expanses of every part of the alimentary tract of the cat leave me in no doubt that this principle is one proper to the vertebrate nervous system.

what I have said of the mode of termination of the nerve fibrils in the myocardium, it constitutes a special problem, the full discussion of which I reserve for a future contribution in which I propose to advance further evidence as well as to review the work of past investigators.

NOTE.—The above paper, embodying some of the results of work commenced in 1924, was withheld from publication pending the appearance of Dr Woollard's paper[1] on the effect upon the nerves of the heart of removal of the stellate ganglia. In so far as it encroaches upon the wide field covered therein, it supports Woollard's description of the general characters of the innervation of ventricular muscle, but disagrees with his findings in the following two particulars:

(1) Isolated nerve cells in the course of the nerve bundles do appear subpericardially below the atrio-ventricular groove. Those which I have seen have not the typical appearance of the large cells with myelinated axons commonly described as "encapsulated," although they possess a much more complicated structure than most cells with unmyelinated axons. A representation of such a cell appears in Fig. G, where its abnormal appearance is evident. It may be, however, that the abnormalities which I have found to occur in the reaction of cardiac tissues to intra-vitam staining produce a misleading appearance in the cells. In no tissue have I found the optimum staining of the different parts of the nerve elements to occur simultaneously. In addition to cells of the type figured there are very small, cell-like bodies to be found, with their long axes concurrent with those of the nerve fibres in the course of the fibres, either isolated or in bundles. Their precise nature I am unable to determine.

(2) The question of the ultimate termination of the nerve fibres is one of great difficulty. In view of their large size and rarity in the field, it is impossible to accept the fibres of Woollard's Fig. XI as anything more than relatively large penultimate branches of the nerves. His Fig. XII, also, if intended to represent the actual mode of termination of the nerves, is unconvincing, some of the fibres terminating in small swellings, while others fade away indefinitely. Subsequent investigation, if it modifies the plan presented in my Fig. A, will probably do so by making the association between the nervous and the muscular elements more rather than less intimate and extensive than is there represented.

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DESCRIPTION OF FIGURES

Fig. A. Terminal intra-muscular nerve fibrils, ventricular muscle of cat. Intra-vitam methylen-blau. Zeiss 2 mm. apo. 0·1 objective; Oc. K. 12. Camera lucida drawing.

The preparation shows two types of termination, both of which are intra-muscular: *n.* with intimate relationship to the nucleus (*nuc.*) of the muscular syncytium; *n′.* without this relationship. The fibril *n.* has a short but complicated intra-muscular course; *n′.* has a longer and simpler intramuscular course; *p.* plexiform ramification external to entry of neurofibril into syncytium; *p′.* plexiform ramification in undifferentiated protoplasm near nuclear pole.

The positions of the muscular striae are represented accurately. The heavier dots represent the regular markings which constitute the dark bands. Note at *nds.* the minute neural nodes replacing the characteristic muscular markings, and, elsewhere, the correspondence of the transverse neurofibrils with the dark bands of the muscle.

Fig. B. Result of plotting separately, with the aid of drawing apparatus, the neural and muscular stained elements: nerve fibril and nodal markings in red, markings of dark band of muscle in black. At *n.* neural nodes replacing contractile elements. At *n.* the markings, although on the course of the nerve fibril, are indistinguishable from the muscular markings. This drawing is also a demonstration of the intra-muscular course of the neuro-fibril, which is represented diagrammatically in B (b).

Figs. C and D. Fragments of intra-muscular nerve fibrils in the human ventricle are shown in both of these drawings. *a.* muscle nuclei; *b.* endothelial (endocardial) nuclei; *c.* blood spaces; *n.* neurofibrils.

Fig. E. Nerve-bundle in human myocardium, with fine fibrillary branch to muscle.

Figs. C, D and E. Ranson's pyridine-silver technique.

Fig. F. Microphotograph of "nerve-ending" in fibre of M. gastrocnemius of the cat. Preparation by Ranvier's gold-chloride method, counterstained with haemalum. Differential staining of the nervous and muscular elements was well shown. *N.* hypolemmal nucleus; *N′.* nuclei of "sole-plate"; *A.* processes of axis-cylinder ramifying hypolemmaly. Note how the nerve processes invest the two nuclei situated most centrally. *Cp.* nuclear relation of intra-protoplasmic plexiform ramification in Fig. A.

Fig. G. Nerve-cell on the course of a sub-pericardial fibre in relation to the ventricular muscle.

Diagram to illustrate the view advanced concerning the nature of neuro-muscular continuity demonstrated for the vertebrate heart. Those parts in black give diagrammatic expression to the theory of developmental continuity between the neural and myoepithelial elements advanced by Graham Kerr, in consideration of his observations of early stages in the development of *Lepidosiren*. Comparison with Fig. A will reveal the trivial nature of the modification whereby I have been able to bring the diagram into conformity with my observations on the vertebrate heart. Nerve fibril in green.

N.C. Ganglion cell.
M. Myoepithelial cell (Graham Kerr).
N.F. Nerve fibre.
Nuc. Nuclei of protoplasm common to neural and myoepithelial elements.
C.F. Contractile fibrils in myoepithelial cell.
Ntp. Terminal neurofibrillar plexus in undifferentiated sarcoplasm.
Ntl. Terminal nerve elements replacing contractile elements.

ANOMALIES IN THE DEVELOPMENT OF SALIVARY GLANDS

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During the session 1925–6, out of 90 bodies put out for dissection, two showed defects in the development of the salivary glands. Such defects are exceedingly rare in the human subject, and we could not trace any such cases hitherto recorded in the journals of anatomy.

Case 1. *Absence of parotid glands on both sides of the face*

This abnormality was seen in the body of a fairly well-built adult male subject. The absence of the Stensen's duct drew our attention to the condition of the parotid glands. The skin over the region of the parotids was entire and showed no marks of any injury or operation. A careful dissection was made over the whole region to find out if there were any traces or rudiments. The entire parotid space was filled with fatty areolar tissue through which passed the facial nerve, external carotid artery and the post facial vein which usually course through the parotid substance. The facial nerve divided behind the posterior margin of the ramus of the mandible and the branches entered the face by winding over its rounded margin. The other salivary glands were dissected out and found normal both in size and shape.

Case 2. *Absence of submaxillary gland on one side*

This was observed in the body of a middle-aged female. The gland and its duct were entirely absent on one side and the external maxillary artery which usually passes through a groove in the posterior border of the gland was conspicuously seen winding over the lower border of the mandible. The gland on the opposite side showed a slight increase in its size. All other salivary glands were found to be normal in size and shape.

These congenital defects of salivary glands in the cases noted must necessarily be due to an anomaly in embryological development. The salivary glands arise as buds from the ephithelial layer of the primitive mouth. The parotid, the earliest to appear (sixth week), forms in the lateral or the bucco-alveolar recess. The parotid duct is at first a groove, but later becomes a canal by the enclosure of the groove. The submaxillary and the sublingual glands arise in the hollow between the tongue and the mandibular arch; first

two furrows appear, the medial for the submaxillary, the lateral for the sublingual. The gland tissue is formed by extensive budding of part of the epithelium of the furrow and the duct from the rest of the epithelium which, surrounded by the invading mesoderm, forms a cord, and later becomes canaliculised. This is the way of usual development. But what factors in early foetal life prevent such development and lead to anomalies is hard to guess. These glands are accessory to the function of mastication and are hence developed only in Mammals. The facts that they are absent in the lower Vertebrates and that they may be removed without any harmful effects in the lower Mammals throw some light on the possibility of such defects being consistent with a healthy life.

In conclusion we wish to express our indebtedness to Dr S. Swaminathan, L.R.C.P., L.R.C.S., Professor of Anatomy, Madras Medical College, for his kind permission to publish the above notes.

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REVIEWS

Heredity and Eugenics. By R. Ruggles Gates, Ph.D., F.L.S., Professor of Botany in the University of London and Head of the Department of Botany at King's College. (London: Constable and Co., Ltd., 1923.) Pp. x + 288. Price 21*s.* net.

We may say at once that *Heredity and Eugenics* is a book which every anatomist should read and keep by him for reference. Professor Gates has complained that the men whose business it is to study and teach the structure of the human body have shown little interest in the processes which underlie the transmission of characters from parent to progeny, and it must be admitted that there are grounds for his complaint. He has therefore done for anatomists what they ought to have done for themselves—brought together the scattered observations relating to the transmission of parental characters—both structural and functional—from one generation to another and surveyed the results with the eye of a professional student of heredity. Particularly valuable is his full list of papers and other sources of information which have yielded the facts incorporated in his text. We sincerely hope that a call for new editions will permit him to keep this work abreast of progress.

It would be out of place in this *Journal* to enter into a detailed exposition or criticism of Professor Gates' work. Developmental abnormalities provide the majority of the examples for the exposition of Mendelian inheritance, and even in their case, as Professor Gates has frequently to admit, the fit between expectation and realisation is not perfect. He has drawn very largely on the literature which deals with congenital malformations of the hand and foot—particularly various forms of brachydactyly. As we come to know more of these cases we see that they are not the isolated discrete conditions we at one time thought they were but form a continuous series, shading from one extreme to another. We are particularly glad to note that Professor Gates clearly perceives that the "factors" which regulate the form and action of the various parts and organs of the human body are infinite in number and that progress in the understanding of the machinery of transmission is kept back because we are so ignorant of the extremely complex machinery which underlies development and growth. Many of the problems which now puzzle geneticists will be solved not by the student of heredity but by the experimental embryologist and biologist. More particularly are we glad to find a Eugenist who has grasped the enormous complexities which beset the path of those who would set the world to rights by selective breeding.

Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen. By CONSTANTIN VON ECONOMO and GEORG N. KOSKINAS. With 162 partly coloured text-figures, and an atlas of 112 micro-photographic tables. (Vienna and Berlin: Julius Springer, 1925.) Price 600 Marks.

When during the first decade of this century the evidence was produced definitely to establish the reality and importance of the anatomical localisation of the cerebral cortex, it was inevitable that some day a comprehensive survey of the human cerebral cortex would be made. Preliminary surveys had been made by a series of investigators, but what was needed was a thorough examination of the various cortical territories and a critical comparison of the results obtained by different methods for the purpose of compiling a reliable and standard charting of the cerebral cortex. This enormously difficult and laborious investigation was begun in the year 1912 by Professor Constantin von Economo in the laboratories of the Psychiatric Clinic in Vienna, and seven years later Dr Georg Koskinas, who is now the Assistant of the Psychiatric and Neurological Clinic in the University of Athens, began collaborating with Professor von Economo to produce this great work, which really marks an epoch in the history of these studies. For the authors have brought to their work not merely superb technical skill and enormous patience, but they have dealt with the history and the literature of the subject with rare judgment and impartiality, and in particular a freedom from national bias.

The Atlas consists of 112 micro-photographs, each of them 1 foot $3\frac{1}{2}$ inches square, and no praise would be too high for the technical perfection of the photographs, upon which the authors and the publisher deserve the highest commendation.

It can be confidently said that such a survey will not have to be done again, and that this work will become a standard treatise of reference on the topography of the human cerebral cortex. No doubt in the future much detailed work will be done upon particular regions, perhaps introducing small points of modification, but the work as a whole is bound to stand as a permanent achievement.

The authors give an excellent summary of the history of this subject starting from the pioneer work of Meynert (1868), to whom they naturally refer with particular pride as a former head of the school in which their own work has been done. After referring to the work of Betz (1874) they pay due tribute to the work of Bevan Lewis (1868–1880) in this country, and Hammarberg in Sweden (1895). After the experimental work of Ferrier, however, this subject fell into neglect, largely because Bevan Lewis's distinctions between the pre- and the post-central convolutions did not seem to harmonise with the results obtained after electrical stimulation, when both the post-central and the pre-central gyri seemed to be excitable. This error was encouraged by the fact that in the myelogenetic investigations of Flechsig (1896–1920) these two

areas became medullated simultaneously. In the year 1900, however, the more exact experiments of Sir Charles Sherrington created a revolution in this field of work. He showed that when proper precautions were made the excitable area was confined to the region in front of the central sulcus, so that the results of physiological experiments were then found to agree with the histological difference recorded more than twenty years previously by Bevan Lewis. Hence at the suggestion of Sherrington, Dr Alfred Campbell began his work, and made the first histological chart of the whole of the human cerebral cortex (1905), in contradistinction to the earlier myelogenetic charts of Flechsig. Of course before Campbell's work was done Bolton (1900) had already mapped out the distribution of the calcarine cortex. At the same time that Campbell was doing his histological work I began to map out the areas by the combination of the histological and naked-eye methods of study, beginning like Bolton with the calcarine cortex, but I soon found that the process of mapping could be done with greater precision by means of the naked-eye observations, which had the further advantage of enabling a large number of specimens to be studied and compared one with the other.

My first complete chart was published in this *Journal* in 1907, a fortnight before Brodmann's complete chart of the human brain, based upon the histological study of an individual specimen, made its appearance. I refer to these matters because in the present treatise the authors adopt the nomenclature which I then suggested, and their own charts are essentially a compromise between what I described as the average condition of one hundred brains and the individual specimen described by Brodmann. They deal very fully with the important pioneer work which Brodmann did, and give due credit to him for it. In particular they present the evidence of their own investigations. They compare their charts of the distribution of the cortex areas not only with all the foregoing work which has been just enumerated, but also the work of the Vogts, of Cajal, of Kaes, and of Jacobs. The work contains a detailed account of the histological characters of each area, with elaborate measurements and comparisons of the analysis of its stratification. There is also a very useful summary of the work which has been done to establish the connections between different parts of the cortex and the rest of the nervous system.

A great encyclopaedia like this, whose value depends upon the wealth of the detailed information it provides, does not lend itself to abstracting, but it can be said with truth that it represents a reliable book of reference giving an impartial and full account of everything that has been done up to the present on the anatomical localisation of the human cortex, together with a summary of the comparative work, and in particular the work of Brodmann. It also gives a summary of the histogenesis of the cerebral cortex and excellent figures to illustrate it. The treatise is such a wonderful achievement, both in the accuracy and completeness of the information it gives, that one refrains from criticising it, especially as the matters that might call for correction are in every case more or less trivial.

All that I need say further is that the authors and the publisher deserve the real thanks of anatomists, for having provided so eminently trustworthy a book of reference to a subject the literature of which is rapidly getting out of hand.

With regard to the Bibliography, the authors have restricted it to quite reasonable proportions, giving only the works which really matter in the history of the subject.

G. Elliot Smith.

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